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PRINCIPLES OF PLANT AND ANIMAL PEST CONTROL

VOLUME 3

Insect-Pest Management and Control

SUBCOMMITTEE ON INSECT PESTS
COMMITTEE ON PLANT AND ANIMAL PESTS
AGRICULTURAL BOARD
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Volume 1 Plant-Disease Development and Control
Volume 2 Weed Control
Volume 3 Insect-Pest Management and Control
Volume 4 Control of Plant-Parasitic Nematodes
Volume 5 The Vertebrates That Are Pests: Problems and Control
Volume 6 Effects of Pesticides on Fruit and Vegetable Physiology

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Foreword

The objective of the project on plant and animal pest control was to outline, for each of the several classes of pests, the principles of control where these are established; to call attention to effective procedures where true principles are not yet established; and to indicate areas of research that appear to warrant early attention. The reports are not intended to be textbooks in the usual sense, nor encyclopedias, but are intended to deal with basic problems, the principles involved in controlling pests, and the criteria that should be considered in conducting research and in evaluating published information. Specific instances of control practices are cited only to illustrate principles and procedures. It is hoped that these reports will be useful to researchers at all levels, to pest-control agencies, to administrators seeking guidance on priorities for application of resources, and to general field workers in the United States and elsewhere.

The National Academy of Sciences selected a committee of outstanding scientists to represent the diverse aspects of the problem and assigned to them responsibility for carrying out the project. To assist that committee, six subcommittees of specialists were appointed. Appropriate members of the parent committee were assigned as liaison members of the subcommittee, and in due time all reports were reviewed by the parent committee.

Some seventy scientists have collaborated over a four-year period to produce this series. Many others have contributed, to a lesser degree, in preparing statements and in reviewing and commenting on drafts of individual sections. Final responsibility for the content of these volumes rests with the parent committee. The Agricultural Board, under whose direction the Committee on Plant and Animal Pests operated, has reviewed and approved each manuscript.

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Preface

The war between man and insect pests never ends, but man has made many advances in pest management and control. The many kinds of insects that affect man's health and welfare vary in their ways of life and adapt to changing conditions, including those brought about through man's efforts to control the pests. Control methods effective against one type of insect pest are not necessarily useful against another. Occasionally, a single method provides adequate control, but usually a combination of methods is better. One of man's greatest advantages over insect pests is the ability to shift and combine controls faster than insects change through mutation and natural selection. Pest management utilizes this advantage.

Although among man's most important enemies, insects are also among man's best friends. We could not envision a world as we know it today without the insect parasites, predators, and diseases that attack destructive species; without insect pollination of crops; and without the role that insects play in our complex ecological system.

The chief aim of economic entomology is to regulate the abundance or prevent the establishment and spread of insects that are harmful to man. Many principles of insect-pest management and control have guided efforts to achieve this aim. This report describes the principles, both the old and the new, and gives control measures appropriate to each.

Members of the Subcommittee on Insect Pests, who represent major aspects of entomology, planned this report and prepared certain parts of it. Other scientists, responding to the Subcommittee's invitation, contributed material bearing on their various disciplines. The Subcommittee expresses deep appreciation to the following persons for substantial contributions: P. Andrilenas, USDA; F. S. Arant, Auburn University; W. L. Baker, USDA; W. F. Baldwin, Atomic Energy of Canada, Ltd.; B. R. Bartlett, University of California, Riverside; A. H. Baumhover, USDA; M. Beroza, USDA; A. W. A. Brown, University of Western Ontario, London, Ontario; P. S. Callahan, USDA; R. G. Dahms, USDA; H. V. Daly, University of California, Berkeley; H. O. Deay, Purdue University; P. DeBach, University of California, Riverside; G. C. Decker, University of Illinois (retired); R. L. Doutt, University of California, Berkeley; J. Drew, USDA; T. Eichers, USDA; J. L. Eschle, USDA; A. Fox, USDA; S. Friedman, University of Illinois; H. Frings, University of Oklahoma; J. C. Gaines, Texas A & M University; R. L. Giese, Purdue University; A. Gieser, USDA; H. H. Golz, American Cyanamid Company; W. J. Hayes, Jr., U.S. Department of Health, Education, and Welfare; L. S. Henderson, USDA; L. A. Hetrick, University of Florida; B. Hocking, University of Alberta; C. S. Holling, Canada Department of Forestry; M. Jacobson, USDA; H. R. Johnston, USDA; J. Kelleher, Canada Department of Agriculture; D. R. King, USDA; L. E. LaChance, USDA; H. Landani, USDA; F. R. Lawson, USDA; E. J. LeRoux, Canada Department of Agriculture; G. E. Lynn, Dow Chemical Company; F. G. Maxwell, USDA; W. C. McDuffie, USDA (deceased); J. J. Menn, Stauffer Chemical Company; R. L. Metcalf, University of Illinois, Urbana; H. A. U. Monro, Canada Department of Agriculture; S. O. Nelson, USDA; J. W. Peacock, USDA; R. J. Pence, University of California, Los Angeles; R. W. Rings, Ohio State University; W. E. Robbins, USDA; G. G. Rohwer, USDA; C. H. Schmidt, USDA; R. F. Smith, University of California, Berkeley; T. R. E. Southwood, University of London; L. F. Steiner, USDA; A. L. Turnbull, Canada Department of Agriculture; R. van den Bosch, University of California, Berkeley; P. H. Wooley, Michigan State University; D. P. Wright, Jr., American Cyanamid Company.

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CHAPTER 1

Introduction

The objectives of insect-pest management and control are to create and maintain situations in which insects are prevented from causing significant problems. These objectives may be achieved by preventing the establishment or spread of insect pests, by controlling established pest infestations, or by keeping infestations at levels at which little or no damage or annoyance occurs. These should be accomplished at the lowest possible cost and without hazards to man or the desirable components of his environment.

PURPOSE AND SCOPE

The purpose of this book is to present the principles involved in various methods of insect-pest management and control in fields, forests, and urban and suburban communities. It was planned to interpolate recent attitudes and philosophies with the established principles and techniques that have served as the foundation for past pest-control programs. This approach includes an introduction to the ecological background underlying pest management, a discussion of the entire spectrum of control methodology, and the blending of these methods into dynamic systems of pest management. Principles, background knowledge, and guidelines are discussed to show the types of control that may be suitable for representative insect-pest problems. These are clarified with examples of pest control methods. The information is intended for use in selecting the most promising approaches in the development of effective pest management and control measures. The training needs and general organizational structure necessary to foster further progress in the refinement and application of this new philosophy of pest control are discussed. Attention is addressed to the economic rationale concerned with controlling pest infestations. While insect-pest control is the main topic, applications and practices of the control of other pest organisms customarily dealt with by entomologists are also discussed.

Having presented discussions on well-established concepts and current hypothesis, the report points out areas where additional or new research is needed to modify, extend, develop, or perfect the present application of the principles involved.

FACTORS IN INSECT-PEST PROBLEMS

There are thousands of species of insect pests spread over most of the areas of the earth where poikilothermic animals can live. Each species of pest is limited to those accessible areas that provide it with food and other biological and physical essentials.

It is estimated that in the United States 150 to 200 species or complexes of related species frequently cause serious damage. From time to time, 400 to 500 additional species are pests and may cause serious damage. Approximately another 6,000 species of insects are pests at times but seldom cause severe damage. Other countries throughout the world are infested with many insect pests.

Migrations of insects may occur as a result of overcrowding, inadequate food, or weather unfavorable to further local increase, or when the insects reach a migratory state in their life cycle. Distances covered range from a few feet to many miles. Insects may attack several crops or only one.

Expansion in world transportation has increased the likelihood of insect pests moving from one area to another. Much shorter transit times often favor the survival of pests. The problems in preventing the spread of insect pests are becoming more complex as a result of rapid changes in transportation.

Some species of insects are pests throughout the year, others only at certain seasons. Insect pests may be active certain years and not others. Harvesting a crop may change the distribution of insect pests by forcing them to move to other crops that they would not normally infest. The factors affecting distribution and activity are variable, so that the distribution of insect pests is constantly changing. In spite of this, the same insect pests often damage the same crop or crops in the same areas year after year. Variations in insect distribution and activity are important factors for consideration in the development of economical and effective insect-pest management and control programs.

The rate of reproduction of insects varies, but in general a great reproductive potential is characteristic of most species. The length of a generation differs. Death of adults before completion of egg-laying, and mortality of eggs, larvae, and pupae because of desiccation, starvation, parasites, predators, diseases, and other adverse factors, greatly reduces the number of insects produced under most environmental conditions. However, the high potential for reproduction of insect pests remains, and a population explosion of many species can be expected from a low-density level whenever suitable environmental conditions occur or control slackens.

Insect pests have great adaptability and have adjusted to many ecological conditions and situations throughout the world. Not only have they become adapted to most opportunities for existence in the past, but they are continuing to adjust to changing man-made or natural ecological situations. An important adaptation by insect and mite pests is the ability to develop resistance to pesticides. This is discussed in Chapter 16.

Changes in cultural, agricultural, and economic patterns throughout the world have had a profound effect on insect-pest management and control. The realization that certain insects are carriers of organisms producing diseases in man has created insistent demands by the informed public that control methods be developed and used effectively to prevent the spread of such pests. The public also insists that control measures not have deleterious effects on man or the environment. There is a demand for control of mosquitoes, flies, and other annoying insects in urban, suburban, and recreational areas. In dwellings, restaurants, hotels, motels, and certain other buildings, the presence of even an occasional insect may be considered undesirable.

The change to continuous croppring systems over wide adjacent areas has created serious insect-pest management and control problems. The demand for agricultural products unblemished by insects has intensified the problems. Producers are subject to legal limitations on the amount of pesticide residue that is permissible on or in their products. Thus, they must balance legal requirements with consumers' demands. Agricultural and forest operations are highly competitive, and the margin of profit on many products is small even when maximum production is obtained. The small margin has greatly stimulated the demand for economic insect-pest controls. This subject is discussed in Chapter 18.

Certain pesticide residues may remain in the environment for years. More information is needed about food-chain concentration and practical ways of eliminating detrimental effects of pesticide residues that may remain in the environment after the pesticides have served their purpose. The pervasive nature of a few pesticide residues in the environment and in plants, animals, and man is justifiable cause for concern. This matter received the attention of the President's Science Advisory Committee in the United States, and its findings appear in the *Report of the Environmental Pollution Panel* issued in November 1965. The report discusses the value of pest control as well as the hazards of pesticide use.

DAMAGE FROM INSECT PESTS

Insects are pests when they reduce the quantity or quality of food, feed, forage, or fiber during production; damage commodities during harvesting, processing, marketing, storing, or use; transmit disease organisms to man or valuable plants or animals; injure or annoy useful animals or man; damage ornamental plants, lawns, or flowers; or damage homes and other personal property.

During the production of most food, feed, and natural fibers essential to man, insects are continuously destroying a part of them. All types of crops, and other plants such as flowers, ornamentals, and lawn grasses, are damaged by insect pests attacking the roots, stems, leaves, and fruiting parts. Plant tissues are destroyed, and toxemias may occur. Both wild and domestic animals are annoyed and injured by insects and related pests. Insects also spread organisms that produce many serious plant and animal diseases.

Insects cause widespread damage to agricultural and forest products during storage and distribution. Large amounts of stored grains are damaged both by actual consumption of the grain and by contamination with whole insects, insect fragments, and feces. The contamination of food by insects is a constant source of loss and concern. Insect fragments in packaged food are often interpreted as indicating that the food has been processed under unsanitary conditions. Insects may occur in conspicuous numbers in food in sealed packages even though the food appeared free from infestation when packed. Termites can cause serious damage to wood used in buildings and to wood products. They are a constant threat in warm climates. Species of termites once confined to restricted areas of the world are now spreading into new territories. Such species increase the hazard of termite damage.

Malaria is spread among humans by *Anopheles* mosquitoes carrying the causal organism; other human diseases result from insect-borne pathogens. Insects cause direct injury to man by their bites and stings and by contact. Salivary secretions injected during the feeding process may cause lingering irritation at the site of the bite. Some individuals show marked local reactions to certain insect bites. Also, an insect bite offers an opportunity for pathogenic organisms to penetrate the skin and cause serious infection. Some hymenopterous insects, such as wasps and bees, inflict stings that cause pain and swelling. Allergic persons may die from a sting. Certain lepidopterous larvae have urticarial hairs that cause dermatitis when they contact the skin, and some of the blister beetles cause a blistering of the skin.

The popularity of recreational areas is greatly diminished by the presence of chiggers, flies, mosquitoes, wasps, and other annoying pests. A human-disease epidemic spread by insect-borne pathogens, or the presence of numerous biting flies, in a resort area may cause widespread cancellation of reservations, resulting in heavy financial losses. Insect pests in the yard around a dwelling are very objectionable, and people go to considerable expense in an effort to control them.

Although most insects do not harm man directly, some people have an illogical fear of them. This state of fear may be reduced when an individual learns more about insects, their habits, activities, and behavior. The presence of a few harmless insects may lead to excessive or unnecessary use of insecticides.

In making estimates of losses from insect pests, it is very difficult to obtain information on any but major pests that repeatedly cause damage. The average annual loss from such insect pests and the cost of control in the United States during the period 1951–1960 is estimated at about $6.8 billion. Of this total, a loss of $6.1 billion was from crop, rangeland, turf, ornamental-plant, forest, forest-product, stored-product, livestock, and poultry insects, and from insect pests of honey bees. These figures do not include crop losses resulting from sporadic insect pests intermittently causing damage in an occasional year, which may be severe in a field, an area, or a region. A few estimates of average percentage losses from insects during production in 1951–1960 are: alfalfa for hay, 15%; corn, 12%; apples, 13%; cotton, 19%; oranges, 6%; rice, 4%; and soybeans, 3%. Estimates of loss during storage are 5.5% for corn and 3% for wheat. Average losses for a crop or commodity tend to hide the very high losses that may be suffered by individual producers or handlers. The average annual estimated cost of insect-pest control in the United States in 1951–1960 was $731 million. Economics of losses are discussed in Chapter 18.

When most of the people in the United States lived on farms, insect damage was taken for granted as part of the normal hazard of crop and animal production. However, with modern operations, the difference between a 5 and 10% loss can easily represent the difference between a profitable and an unprofitable farming operation. When faced with the prospect of a loss from insect damage, the modern producer needs to know whether the potential loss will be larger than the cost of control and approximately the difference. Better methods for determinating insect losses and more accurate estimations of probable insect damage in specific situations are needed.

METHODS AND ECONOMICS

Insect pests can be controlled by a variety of methods. The first principle in insect control is the correct identification of the pest. Identification of insects is discussed in Chapter 2. Correct identification provides a key to published information on the life history, behavior, ecology, and other factors important in the development of control measures for a pest. Once an insect pest has been correctly identified and the available information assembled, the applicability of various methods of pest management can be considered. In evaluating different methods of control for a particular pest, the harmless level of infestation, or the economic threshold, should be considered.

The ecological factors affecting insect populations are of major importance in insect-pest control. All available knowledge about the biotic and abiotic characteristics of the environment affecting the pest should be used in weaving a pattern of insect control for a specific pest in a specific place. Figure 1 shows some of the components of the environment, the physiological status, and the process of development that affect growth, reproduction, and behavior of an insect. The manipulation of ecological or physiological factors by man may produce effective ways of controlling pests. (See Chapter 17 for a discussion

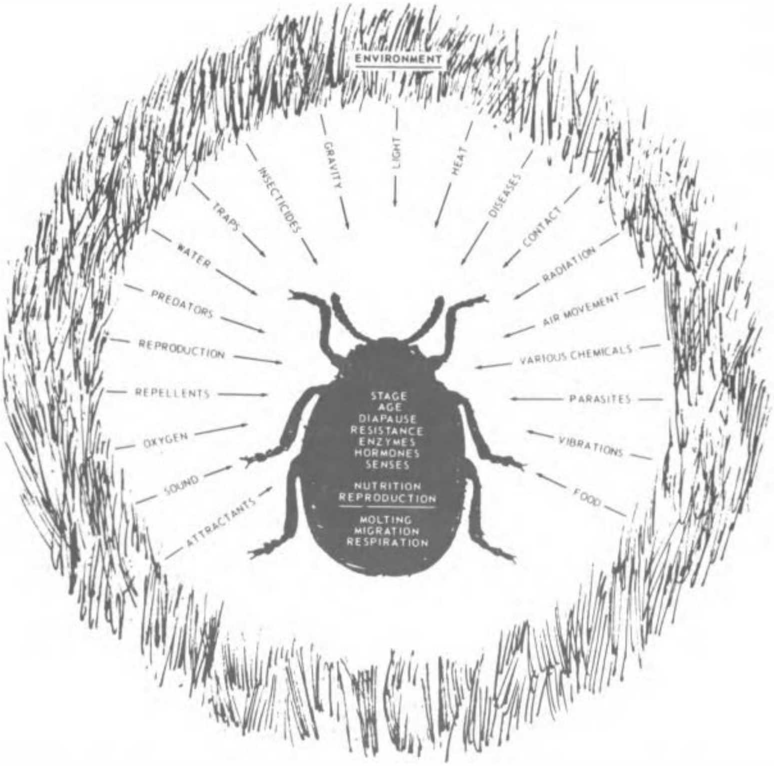

FIGURE 1 Factors affecting insect activities. (From Agricultural Science Review 3:1, 1965.)

of integrated control.) An understanding of the ecological factors affecting an insect-pest population is essential to planning or improving a control program.

Adequate surveying or inspection of crops, animals, and products subject to insect damage is of primary importance in reducing the damage and the cost of control. This procedure permits detection of incipient or low-level infestations before they spread or develop to damaging proportions. Thorough inspections by trained personnel reveal whether control measures are actually needed and point out potential trouble spots or conditions especially favorable to insect-pest development, so that they can be eliminated or corrected. In planning the control of major insect pests, provisions must be made for obtaining adequate information on their activity and economic infestation levels (see Chapter 3). Research is usually needed to determine the best methods of obtaining and interpreting the required information.

Successful insect-pest management and control are profitable. To determine the possibility of making a profit from pest control, it is first desirable to determine the amount of pest damage. It is then possible to estimate what could be spent profitably in reducing the damage. The next step is to determine the most efficient approach to the problem. All available methods of insect-pest management and control should be considered. These methods are discussed in detail in the following chapters.

Good control must be economically sound for both immediate results and long-term effects. A control practice that builds up future problems should be avoided even though it gives excellent immediate results. A pesticide treatment that destroys the natural enemies of the pests that feed on a crop may allow the pests to multiply at a rapid rate after the lethal action of the pesticide has disappeared. It may also create a situation in which other pests, formerly held to low infestations by predators, parasites, or diseases, can increase at a rapid rate and become economically important.

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CHAPTER 2

Identification and Classification

An insect pest is a biological species (or population thereof), and entomologists should understand what this means in terms of pest management and control.

Insect classification provides a framework within which all knowledge regarding each species may be recorded. To the extent that the classification reflects genetic relationships, it permits useful generalizations and contains a high degree of predictability regarding pest species and their ultimate control. This predictability becomes more important as pest control becomes more complex.

In order to retrieve reliable data from the classification, or to utilize its predictability, the classification must be accurate. Thus, correct identification of a pest species is the first step in scientific pest control. It provides a key to published information on the life history, behavior, and ecology of the insects, and to other data important in the development of control measures. When adequate published data regarding a particular pest species do not exist, the identification may furnish useful information through leads derived from published data on related species. Correct identification is also an essential element of plant-quarantine enforcement, exploration for foreign parasites and predators, search for insect resistance in crop varieties or animal breeds, and selective control procedures of all kinds.

Initial taxonomic identification of pest species should be made by specialists in taxonomy. Where sibling species, genetic strains, and biotypes involve pest species or their natural enemies, precise identification of these may be required in connection with control programs. In such cases, identifications should be made by laboratory or field biologists familiar with the physiological, behavioral, ecological, or genetic characteristics of the populations concerned.

Although traditional methods of identification and data retrieval have served entomologists reasonably well, taxonomic methods must become mechanized and data retrieval systems must be vastly improved if the needs of entomologists are to be met satisfactorily in the future. Some suggestions for automated approaches to these problems are given later in this chapter.

BIOLOGICAL-SPECIES CONCEPT AND MANAGEMENT

To appreciate the problems confronting the systematist in classifying organisms and to anticipate certain problems in pest control, one must understand the nature of the biological species. Only a brief discussion can be included here; for fuller treatment the interested reader is referred to recent general works on evolution appearing in the bibliography at the end of this chapter. While the higher categories of the familiar biological classification (e.g., genera, families, and orders) can usually be recognized by characters observable in a single organism, the recognition of a species includes more than the tangible features of the specimen at hand. Modern systematics stresses the importance of the reproductive relationships among the individuals of a species rather than their anatomical similarities alone. This emphasis stems from the fact that the transmission of the genetic material through reproduction provides the only continuity between organisms in time and in evolution. The factors influencing the transmission of genetic material are therefore of interest in understanding the process of evolution and in scientific control of pests.

Most of our knowledge concerning the genetics of populations has been deduced from the Mendelian laws of heredity. These laws apply only to sexually reproducing organisms or "Mendelian" populations. Each gene may exist in one of several states (or alleles). The relative frequency of a given allele in a Mendelian population may be computed, and predictions may be made about the frequency to be expected in subsequent generations under specified circumstances. One important deduction is that in the absence of certain modifying forces, the original frequencies of the genes in a large population can be expected to remain virtually unchanged in generation after generation.

Changes in gene frequency in a large population may be expected if some of the genes in question mutate to another allele, some individuals possessing the gene are removed by natural selection before reproducing; or some of the individuals possessing the gene migrate from the population, or additional individuals migrate to the population. When a population is distributed over an ecologically diverse region, the joint action of these modifying forces in each different situation leads to unique frequencies of many different genes within each area. Such adaptive complexes may or may not be distinguishable by anatomical differences. Furthermore, the exchange of genes between adjacent populations may be slightly to entirely reduced by physical or biological barriers. Populations thus isolated may be expected to become increasingly distinct and may or may not interbreed with adjacent populations if contact is re-established. Failure to interbreed with adjacent populations is the criterion by which species are defined in theory. A biological species is formed by groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups or by the largest and most inclusive reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool.

The significance of these rudiments of the theory of population genetics may now be examined. First, it should be clear that the reproductive relationships of a species can rarely be determined in practice. Other lines of evidence (similarity in anatomy, physiology, and behavior; and geographic continuity) must be used by the systematist to infer interbreeding unless actual field and laboratory information is available. Conclusions drawn from inferences alone may overlook populations similar or identical in characteristics but reproductively isolated even when in contact. Such populations are called sibling species. Any program of pest control directed against a single species of organism should critically examine the evidence that the populations are conspecific. Similar economic problems may be created by two or more sibling species, and the techniques for control may be adequate for all. However, genetic differences that cannot be shared between the reproductively isolated populations may be important. For example, a specific inherited ability to resist insecticides will be restricted to those populations exchanging genes. Resistance in all other populations, even of the same species, must be developed independently. Control techniques applied to the same species throughout its distribution are actually being applied to different adaptive complexes with different susceptibilities to the controlling agents. Geographic differences in resistance to insecticides provide excellent examples.

Pest conditions are commonly created by insects introduced from foreign countries, where they may or may not be of economic significance. Systematics plays an important role in determining the country of origin, so that native agents of biological control may be sought. The alien insect may be established from a single individual, and its success may be phenomenal. The colonization of new habitats, especially islands, has long been a favorite subject for systematic investigation. The results of these studies are of value in understanding the biology of an introduced pest. In view of the differences in local gene frequencies from place to place within the native range of a species, any small sample of individuals will probably not contain representatives of each of the alleles possessed by the species as a whole. Furthermore, the frequencies present in the sample are not likely to approximate the frequencies prevalent in the original local population. A sample of only one individual represents only a very small part of the genetic variation possessed by the species. Such small samples, however, often provide the initial colonizers of new habitats. Subsequent interbreeding within the small population may further reduce the genetic variation, since some alleles may be lost by chance (a phenomenon called genetic drift). The differences in ecology between the new and native environments drastically alter the selective advantages of the genes in the initial population, and new adaptive complexes are developed. The lack of parasites and predators and the presence of new host plants or animals, therefore, are only part of the explanation of the success of certain introduced insects. The circumstances of the introduction actually promote changes in gene frequency, and the colonizing populations may no longer resemble the native populations in many respects.

The foregoing has been restricted to sexual and cross-fertilizing organisms. This is the most common type of reproduction among insects and is the type about which predictions can be made. However, parthenogenesis, or reproduction without fertilization, is not infrequent, but the theoretical consequences of this type of reproduction are little known. Hermaphroditism, or the possession of both sex organs by the same individual, is known only in the cottony-cushion scale, *Icerya purchasi* Maskell, and certain flies of the family Phoridae.

The critical importance to agricultural entomology of studies of the systematics and evolution of pest species is demonstrated by species and variants of the weevil genus *Hypera* attacking alfalfa in the United States and Canada.

A strain of the alfalfa weevil, *Hypera postica* Gyllenhal, was introduced into Utah from the Old World sometime prior to 1904. In the next 30 years, it gradually spread over most of western North America. This spread was accompanied by the evolution of populations in different parts of its range, (e.g., Lethbridge, Canada; Logan, Utah; and Tracy, California) to the now-different biological entities. Specifically, these entities differ in their response to the physical environment and in their behavior. For example, the Lethbridge weevils do not become active in the spring until the weather warms up to a higher level than that in Utah. This behavioral pattern protects the population from a sudden reversal in temperature and aids in their survival in a cold climate. This biological strain still belongs to the same species.

A different strain of *H. postica* was introduced into the eastern United States sometime in the 1940's. It differs from the western form in a number of characteristics, e.g., cocoon construction, but still seems to be the same species. It has, in a rather short time, spread over much of the area east of the Mississippi River.

A sweetclover-adapted strain (*Melilotus*) of the Egyptian alfalfa weevil, *H. brunneipennis* (Boheman), was introduced into the Yuma Valley of Arizona sometime in the 1930's. It was first thought to be the same as *H. postica.* However, it has widely different climatic adaptations from those of the more northern-adapted *H. postica.* For many years, *H. brunneipennis* remained associated with sweetclover in the Yuma Valley. Then, rather suddenly, it became adapted to alfalfa. Populations increased, and it spread into California. It has become an important pest of alfalfa in southern California and recently moved into the central part of the state.

Larvae of both *H. postica* and *H. brunneipennis* are parasitized by the ichneumon wasp, *Bathyplectes curculionis* (Thomson). It has recently been demonstrated on the basis of defense reactions of the weevils, i.e., encapsulation, that two strains of the parasite exist. The northern California strain of the parasite is only about 10% effective in attacking the southern *H. brunneipennis,* while the southern strain is about 85% effective. The northern strain is over 99% effective in attacking the northern *H. postica,* while the southern strain is about 90% effective.

CLASSIFICATION FOR MANAGEMENT

It has been widely held that one of the principal objectives of taxonomic classification is to provide a convenient filing system for recording facts about the vast array of living plants and animals that constitute the biological phase of man's environment. This viewpoint has been expressed most commonly with regard to the framework, or nomenclature, with which classifications are constructed. This is an important function, but this same function might be accomplished more efficiently and effectively in other ways. Undoubtedly, greater effort would have been made to substitute a better data-filing system if this were, indeed, the principal objective of classification. The present system of biological nomenclature cannot now be easily replaced; until it is, the most immediate problem is to develop more-efficient means for retrieval of data that have been recorded by means of a system discussed later in this chapter.

Another objective of taxonomic classification is to attempt to express, through the nomenclatural system, degrees of relationship among the almost overwhelming variety of populations (species) of plants and animals existing throughout the world. This is accomplished by means of a hierarchy of taxonomic categories (genera, tribes, families, and orders) that are intended to express the degrees of relationship that taxonomic methods reveal. Taxonomists differ on such philosophical questions as whether taxonomic categories, including the species, actually exist in nature, and whether a phylogenetic system (a classification based on probable ancestry) using weighted characters or a phenetic system (a classification based on over-all similarity) using unweighted characters is superior. From the viewpoint of the applied biologist, these philosophical arguments are irrelevant. What is relevant is the extent to which classifications have built-in predictability. Until now, the best classifications arrived at by means of the traditional phylogenetic approach have exhibited a high degree of predictability, which can be and has been exploited in the solution of applied problems. If the time should come when phenetic classifications prove to have generally greater biological predictability, they may prove to be more useful in the applied field. The phenetic approach, having had few practitioners, has not been tried on a scale that would permit such a conclusion.

The built-in predictability of "good" classifications has been used successfully many times in looking for the home of introduced pests in search of potential parasites. The method used has been to search in the center of distribution of the genus. However, if the classification is invalid and the generic assignment is incorrect, the results can lead to failure. For many years, the sugar-beet leafhopper, *Circulifer tenellus* Baker, vector of curly top virus, was incorrectly placed in the genus *Eutettix*. In 1918 the California Commission of Horticulture sent an explorer to Australia to search for the leafhopper and its natural enemies, but the insect was not found there. The United States Department of Agriculture surveyed the situation in Argentina and Uruguay in 1926–1928, and later in Mexico. Again, *C. tenellus* was not located, and no parasites were sent to the United States. As a result of effective systematics, the position of *tenellus* was clarified, and it was shown to be a representative of the Old World genus *Circulifer*. As a result, explorations in Spain and North Africa uncovered both *C. tenellus* and a large number of its parasites, which were liberated in the western United States.

From 1877 to 1937 the red scale, *Aonidiella aurantii* (Maskell), was repeatedly misidentified, and its generic placement was particularly unsound and misleading. For a time this scale was placed in the genus *Chrysomphalus*, mostly a South American genus; therefore, a decision was made to search for enemies of red scale in South America in 1935. In 1937 more-precise taxonomic studies correctly placed red scale in the oriental genus *Aonidiella*, and the most promising natural enemies have been obtained from the Orient.

IDENTIFICATION OF INSECT PESTS

Taxonomic specialists in a position to make primary identifications of pest species or to refer inquiries to other specialists are employed by government agencies such as the United States Department of Agriculture (Insect Identification and Parasite Introduction Research Branch, Entomology Research Division, Beltsville, Maryland, and Washington, D. C.), Canada Department of Agriculture (Taxonomy Section, Entomology Research Institute, Ottawa, Ontario), and Commonwealth Institute of Entomology, London, England; by many state departments of agriculture; and by many universities and museums. A list of taxonomists and the groups of organisms with which they work is available. (See the bibliography at the end of this chapter.)

When the pest has been correctly identified, if it was previously known as a pest, the name will provide a key to published data with respect to its control, not only under its currently used name but also under any others (synonyms) applied to it in the past. If the species was not previously known to be a pest, or if adequate control measures have not been developed, the correct name (and its synonyms, if any) will lead to published information on the insect's life history, behavior, and ecology–important in the development of suitable control procedures. However, correct identification of a pest should not be confused with determining the correct name of a pest. Rules governing the naming of animals and the methods for selecting the correct name, if more than one name has been applied to a species, are contained in the *International Code of Zoological Nomenclature,* published by the International Trust for Zoological Nomenclature (see the bibliography). Also, the International Trust has published official lists of generic and specific names that cannot be changed on purely nomenclatural grounds (see the bibliography). These lists include many names of economically important species, e.g. *Cimex, Musca, Blatta, Nabis, Triatoma, Pulex, Oestrus, Gasterophilus, Hypoderma,* and *Locusta.* However, in addition to scientific names, most pests have common names. A number of useful lists of common and scientific names of insect pests have been published in the United States, Great Britain, Canada, Australia, and Europe (see the bibliography).

A useful guide to published information on insect pests and their control is the *Review of Applied Entomology,* a periodical of worldwide scope, published in London since 1913, which consists of two series, one providing abstracts of papers relating to agricultural entomology, the other, those relating to medical and veterinary entomology. If the pest is well known, information concerning it will probably be found in such a comprehensive work as *Handbuch der Pflanzenkrankheiten.* For North America, the *Index to the Literature of American Economic Entomology* provides a key to much of the published information about pests from 1917 to 1962, and references to important literature on the subject may be found in the *United States Department of Agriculture Yearbook for 1952.* Also, there are many books that discuss pest species. (See the bibliography for some of the most recent ones.)

An important guide to published information on the life history, behavior, and other activities of insects is the classified index in the introduction to the *Insecta* section of the *Zoological Record,* published annually in London, England. Abstracts of much recent literature on insect biology, grouped by orders, may be found in *Biological Abstracts,* which also publishes *B.A.S.I.C.* and *BioResearch Titles,* which provide leads to articles through their titles. Extensive worldwide bibliographies on insects and their activities are available in review articles in *Annual Reviews, Inc.,* published by the Entomological Society of America (1956 to date). Also, regional and world catalogs are available for many insect groups, and these are useful in determining synonymy and, in some cases, in providing references to papers on biology. Unfortunately, few of them are current.

There are numerous examples of the importance of correct identification to pest-control programs. One of the best known involves the epidemiology of malaria in Europe. Prior to 1930, the name *Anopheles maculipennis* Meigen was applied to superficially similar mosquitoes occurring widely over the continent, and these mosquitoes were believed to transmit the organism causing malaria. Control measures were directed against this "species" throughout much of its range. However, careful taxonomic studies eventually showed that the European *"maculipennis"* consisted of a complex of closely related sibling species with different geographical ranges, habitat preferences, and breeding habits. The discovery that not all of these species transmitted the malaria organism explained the anomaly previously observed, that malaria occurred discontinuously within the distribution of what had been considered a single "species." This information made it possible for the first time to direct control measures precisely where they would be most effective.

A somewhat similar situation developed in North America with respect to screw-worm flies. For years, the name *Cochliomyia macellaria* (Fabricius) was applied to flies that laid their eggs in wounds and open sores in man and other animals, domestic and wild, as well as to flies that oviposited in carcasses of dead animals. Control measures involving trapping and burning carcasses failed to reduce the incidence of myiasis caused by flies ovipositing in wounds. Again, taxonomic studies revealed that two species were involved: *C. macellaria* (Fabricius), which bred in carcasses, and *C. hominivorax* (Coquerel), the myiasis-producing screw-worm. Trapping and burning of carcasses was abandoned, and suppressive measures were aimed at the real culprit, ultimately resulting in control by spectacular sterile-male procedures described in Chapter 15.

With reference to the significance of taxonomy in assessing the vector importance of arthropods in the epidemiology of arthropod-borne agents of diseases afflicting vertebrates, many examples could be cited where failure to differentiate closely related species of arthropods has resulted in misleading concepts as to vector roles. For example, early workers for a time confused the African tick *Ornithodoros moubata* (Murray) with *O. savignyi* (Audouin); these two species occupy different ecological niches, often in neighboring sites. At least some populations of the former are very important vectors of organisms causing relapsing fever in man, but there is now considerable doubt that *O. savignyi* transmits organisms that produce the fever.

A more recent example of the need for meticulous taxonomic studies to support research on disease relationships of ticks has been cited, wherein the virus of Quaranfil fever in Egypt is associated with the tick *Argas arboreus* Kaiser, Hoogstraal, and Kohls, a species that would until recently have been identified as the closely related *A. persicus* (Oken). Hosts and distribution of these species are widely at variance.

Although other examples might be cited to illustrate the importance of correct identification in programs involving chemical or physical control, the problem is particularly critical in relation to biological control. For example, the mealybug now known as *Pseudococcus kenyae* LePelley appeared in severe infestations in Kenya in 1923. It was first misidentified as *P. citri*, and, in 1925, unsuccessful attempts were made to introduce its parasites from Italy to Kenya. The pest was later thought to be *P. lilacinus* Cockerell, and it was referred to by this name until 1934. Enemies of *P. lilacinus* and other mealybugs were obtained from Java, the Philippines, Hawaii, and California, and all failed. Finally, the mealybug was correctly recognized as an undescribed species from Uganda, and parasites were obtained from that area; these parasites very quickly and completely suppressed the pest.

SYSTEMATICS AND INFORMATION RETRIEVAL

Stepwise, the general sequence of events that provides access to published reports of a pest is as follows: (1) the preliminary identification to a taxonomic level that will permit the specimen to be sent to the appropriate specialist, (2) the specific identification by a specialist in the taxa concerned, (3) the search for bibliographic citations that may contain information on the species, and (4) the finding of pertinent information contained in each published article. Part or all of each step must then be performed by trained personnel. The time consumed and the competency of the persons involved are important limitations on the speed and relevancy of the information supplied to a pest-control program. Under ideal circumstances, how can this procedure be accelerated and improved? It is convenient to discuss this question with regard to systematics and then with regard to information retrieval.

An automated procedure in systematics should be expected to: (1) determine the characteristics of a specimen, (2) place the characteristics in the computer memory, (3) create a classification of the specimens, (4) create a logical scheme or key to identify a new specimen as one of those previously processed or as a new taxonomic unit, (5) revise the classification and key for each new taxonomic unit, and (6) supply on request any desired information about the characteristics and classification of the taxa included. Steps 2 through 6 are already well within the capacities of modern electronic computers. The number of taxa that may be accommodated, however, is still restricted by the size of the computer memory. Techniques are being developed by systematists and others to automate the classification and identification of an organism once the characteristics are known. To take full advantage of the computer, certain changes may be expected in the structure of classification, the formation of the "key," and the definition and designation of species. A uninominal nomenclature and a numericlature, for example, have been proposed to increase stability of scientific names and to facilitate automation.

Step 1, the determination of characteristics, remains the major obstacle to a fully automated procedure. Characters can, of course, be observed and entered into the computer by a systematist. An automated key with televised illustrations of the alternative choices could be constructed for identification by persons with less training. Similar solutions will have to suffice until the characters can be taken directly from the specimen by a machine. Devices exist for scanning certain parts of the body or microscopic preparations and storing this information in a computer. However, appraisal of the usual morphological features may not be the most desirable choice of characteristics. Ideally, an analysis of the genetic material or "code," or certain biochemical products of the code might be desirable. Such a procedure is under study in bacterial classification, with the prospect of an automated biochemical analysis of a sample and the subsequent automatic identification.

Similar procedures might be applied to insects by utilizing the combined efforts of biochemists, physiologists, and systematists. Considering the enormous difficulties now involved in the identification of compounds in careful physiological investigations, some time may be required before comparative analyses can be made routinely. The effects of age, diet, sex, physiological condition, and geographic distribution will have to be evaluated. Cuticular waxes, for example, might prove unique for a species, as they have for some plants. Patterns automatically derived from gas chromatography or mass spectrometry might serve the purpose of the systematist equally well without necessarily identifying the responsible compounds.

Progress in the area of an automated systematic procedure is retarded not merely by a lack of suitable instruments but also by our imperfect knowledge of much of the world's fauna. The latter problem is especially acute in dealing with insects encountered in pest control. Introductions may be expected from virtually any part of the globe. A fully automated procedure functioning now would only be able to decide that a specimen was new, but further information as to the country of origin, and habits, for example, might not be available.

Turning now to information retrieval, the goal of an automated procedure might be to ask, "What is known about *X*?" and to receive copies or a visual display of the desired information in the desired language. To achieve this end, the actual text and graphic material would have to be placed in the computer; the information in the articles would have to be cross-indexed and, if necessary, translated; and portions of the articles would have to be reproduced on demand. Again, the initial step of placing the information in the computer is the major obstacle. Text and graphic materials are already commonly converted into digital-computer storage and subsequently retrieved in the form of automated commercial printing processes and television. If all present and future publications relevant to pest control were so treated, part of the task would be accomplished. Critical reviews and monographic studies would be especially helpful. Past publications may prove to be only a small part of the total. Selections from these would have to be entered by hand key-punching until an automated reader is developed. Once the text is stored in a computer, it is available for various cross-indexing systems and for translations.

Solutions to the general problems of information retrieval, indexing, and translation are being sought by many groups. Fortunately, some of the problems facing other areas of human knowledge were solved long ago by systematists. The hierarchical structure, the elimination of synonyms and homonyms, the international terminology, and the mutually exclusive taxonomic units are among the attributes of biological classification that greatly facilitate automation. Because of the unitized format of most taxonomic publications, strictly taxonomic information such as descriptions of new species, distribution records, and host preferences could easily be retrieved from a computer. The use of common names adds some complication, but uniform usage as proposed by the Entomological Society of America has minimized this source of confusion in recent publications in the United States. Uniqueness of most of the chemical and commercial names of insecticides simplifies automatic retrieval of information.

Entomologists must now maintain a file of simple or edge-punched cards with an elementary cross-indexing system. Additions to the file are usually made by the chance finding of an article or by routinely searching periodicals containing cross-indexing citations—such as *Zoological Record, Biological Abstracts,* and allied publications; *Bibliography of Agriculture* and *Pesticides Documentation Bulletin;* and *Guide to the Literature of the Zoological*

Sciences. These are necessary aids to information retrieval, but the present procedure suffers a number of disadvantages: (1) not all articles are included; (2) commonly only information in the bibliographic citation is cross-indexed, leaving the specific units of information in the article not indexed; (3) actual text and graphic material must be sought in the original publication; (4) only the simplest systems of cross-indexing can be handled in the individual file; and (5) much effort is duplicated by investigators with similar interests. Catalogs of insect groups are of great benefit to all entomologists in information retrieval (see the bibliography). The initial preparation of a catalog and the updating of its contents are best performed by automatic devices. An automated system, then, is probably both more efficient and less expensive.

Instantaneous identification and information retrieval are not likely to materialize within the next few decades. Pioneering steps must be taken toward solutions to these problems in pest control, not only to take advantage of the technology already available, but to be prepared to utilize the facilities of the future.

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CHAPTER 3

Insect Surveys

The detection of insect and related pests and surveys of their distribution and abundance are essential prerequisites to rational control programs. The details of detection and survey activities vary according to ways in which the resultant data will be used to support specific kinds of control programs, but certain aspects of these activities are basic to all such programs.

The first principle of pest detection and surveys as related to control is that no control measures should be undertaken against a pest unless it is known that the pest is actually present. In many instances, particularly in agriculture, this principle is not followed. A farmer often follows a control schedule blindly, without bothering to determine whether the pest is truly present on his crop. The economic implications of this are obvious, and such wasteful procedures may also result in the needless destruction of beneficial species and the addition of undesirable chemical contaminants to the environment.

After the presence of a particular pest has been confirmed, attention may be turned to the second principle of pest detection: No control measures should be undertaken unless it is known that the pest is present in sufficient numbers to cause economic loss. This presupposes that adequate background research has been done with the particular pest and its plant host to establish the "economic threshold": the population level of the pest that will cause sufficient damage to make control economically desirable. Below this threshold, the cost of control exceeds the value of the portion of the crop protected from damage, and the net result is a financial loss. Above this point, the value of the portion of the crop protected exceeds the cost of control, and money will be saved. The economic threshold varies in time and place throughout the season, and is sensitive to weather, agricultural practices, and market and labor conditions. The determination of a threshold requires economic studies as well as those in biology. It also requires the ability to predict the short-term trend of pest populations; a given population may be increasing toward its economic threshold, but control activities need not be initiated if it can be predicted with confidence that the population will peak and decline below this point.

Detection and surveys are especially important to quarantine and eradication programs. They are discussed in detail in Chapter 4. They are also essential to the success of integrated control systems (Chapter 17).

KINDS OF SURVEYS

All insect surveys are alike in that they attempt to assess some property of the insect to be found over a reasonably large area, and they are extensive in nature. Therefore, they differ from an intensive program carried out on a single population in a limited habitat. The actual property of the fauna measured in a survey will depend on the type of survey. The following broad types may be recognized: qualitative surveys, involving the identification of the different species; quantitative surveys, involving the estimation of the population of one or more species of insect.

QUALITATIVE SURVEYS

Qualitative surveys may cover the whole fauna of a region, as does the "California Insect Survey," or they may be limited to one or more of the following categories: potential pests, actual pests, and natural enemies.

It is theoretically desirable that, when extensive agricultural development is proposed, the potential pests be surveyed along with the soil, vegetation, and climate. Some work on these lines has been done in Russia. However, in the present state of our knowledge it is difficult to determine which species will adapt particularly well to the proposed new crops and conditions. Also, pests that can become economically important in the future may be scarce at the time of the survey and may be easily overlooked in a natural ecosystem. Nevertheless, certain broad generalizations can be made; e.g., the stalk borers of wild grasses will probably attack graminaceous crops. Such information is often valuable in retrospect in interpreting the origins of pest species and in adding to our basic understanding. Thus, some useful information can be gained from a survey of potential pests.

Qualitative surveys of actual pests, although an important initial step in the rationalization of peasant agriculture, seldom provide significant new information in regions where any form of agricultural advisory service has been established for some time. In contrast, a knowledge of the natural enemies of a pest in different parts of its range is an integral and initial component of any program for biological control by importation. In many early biological-control projects, an entomologist made a qualitative survey of the natural enemies of a pest in its supposed country of origin; if any selection of potential control agents for introduction was made, it was based on his intuitive assessment of their roles. As shown below, additional relevant evidence may be obtained by a quantitative assessment of the roles of various parasites and predators. Consequently, whenever possible, a survey of natural enemies for biological-control potentialities should be quantitative as well as qualitative.

QUANTITATIVE SURVEYS

Quantitative surveys involve measuring the abundance of the insect. There are two types of measuring: absolute and relative. Absolute estimates give the number of insects per fixed unit; the unit may be part of the habitat, e.g., leaf or stalk, and give a measure of population intensity, or it may be a unit of square measure, e.g., acre or square meter. The units in which population intensity is measured will change from field to field as well as from season to season. It is always important to measure the number of habitat units per unit of area, so that estimates in terms of population intensity can be turned into strictly absolute measures and vice versa at any time. Population intensity is the correct expression of density for some purposes, but for others absolute population per unit area is more appropriate.

Relative population estimates are obtained by measuring the population, or samples from it, in qualitative units, on the assumption that these units allow comparison from time to time and place to place. Faith in the strict comparability of relative measures is not always justified. For example, differences in the numbers of insects caught in two identical light traps in two areas could be caused by real differences in the actual populations, by variations in activity due to weather, or by variations in the efficiency of the trap. The efficiency of a light trap will be reduced by any lack of contrast between it and its surroundings. Lack of contrast may be due to light from adjacent tall vegetation or to light from other sources, including moonlight. The same types of inaccuracies can influence almost all types of relative measurements, e.g., variations in efficiency and, when the method depends on the movement of the insect, variations in the level of its activity. Weather and climatic variation will influence both.

Relative estimates do, however, play an important role in survey work; compared with absolute estimates, they can usually be obtained at fairly low cost both in terms of apparatus and in hours of work—important considerations when large areas are to be covered. The principal methods of obtaining relative estimates are the use of various traps (light, water, bait, sticky, and interception) and the making of catches per unit of effort, e.g., the number of larvae per 10 minutes of search. Another rather special type of relative estimate is the population index; this is based on either the products or the effects of the insects, not on the insects themselves. Population indices have been widely used in survey work. One of the earliest examples was the regular survey of the fall webworm, *Hyphantria cunea* (Drury), made by counting the number of caterpillar tents seen by the observer while driving along given roads; data obtained in this way have recently been of value in population research. A more widely available criterion is the amount of damage caused by an insect. Certain types of insect damage to forests can now be readily surveyed over a large area by aerial photography, in black and white or in color.

At the outset of quantitative surveys, it is important to select the appropriate stage of the pest for sampling. Since surveys are usually conducted in different areas at different times, the stage selected should be present in the field for as long a period as possible; i.e., its development time should be long. Otherwise, there is the risk that a low count in an area will be caused, not by a low population, but by the insect having already passed through or not having reached that particular stage. However, for most survey purposes, the insect stage selected should be related in abundance to that causing the economic damage to the crop. This is usually the larval stage. The extent to which the egg stage may be used to predict the numbers of larvae will normally be a matter of research in which investigators use methods of analysis described later.

USES OF SURVEYS

The numbers of a pest species over a wide area may be surveyed in relation to (1) damage; (2) various factors influencing population size, e.g., climate and natural and artificial control; and (3) the future size of the population—prediction and the need for control measures.

The special aspects and techniques of these types of quantitative surveys are discussed below, but some consideration must initially be given to the various advantages and disadvantages of the survey method for investigating pest populations.

To study the role of different population factors by using the methods of R. F. Morris or of G. C. Varley and G. R. Gradwell, it is necessary to have at least 10 observations, and preferably many more, with extensive work on a univoltine insect. This will mean more than 10 years of work. It is to some extent possible to use the data from different areas obtained in surveys and thus to substitute space for time and obtain an indication of the roles of various factors in population control much more quickly. Another advantage of surveys is that any justifiable conclusions based on a wide geographical area may be claimed to be sound generalizations; in contrast, if an intensive study is made of one area, this area may turn out to be peculiar in some way, and generalizations from it may be unreliable.

The disadvantage of surveys is that, while gaining so much from their breadth, they of necessity lose depth, and the detailed mechanism of population regulation is not directly revealed, as it may be by the study of a single cohort. Therefore, the role of different factors is assessed by correlation analysis of, for example, the size of the population against a climatic factor or of the amount of damage against population size. Correlation is not necessarily equivalent to causation; thus, although reduction in yield may be closely correlated with increase in insect population, the two may be linked to a third factor, such as drought, which affects the plant adversely and the insect favorably. Therefore, in the ideal program the interpretation of surveys should be confirmed by carefully designed field tests and, in some instances, by laboratory experiments.

DAMAGE SURVEYS

Damage surveys are often important both in the initial intensive stage of an investigation and in routine control projects. The object of the survey may be to determine the extent to which an insect species causes significant economic damage over a wide area. This is sometimes referred to as "pest assessment." The criterion of damage can be reduction in economic value or in yield, or it can be some measure of destroyed or damaged parts, e.g., a "dead-heart count" or a "leaf-tatter index." Damage is measured in one of these ways, and the numbers of the pest in the area are also determined—most appropriately as population intensity, or the numbers per plant or per leaf, although relative estimates will often suffice. The two sets of data, damage and insect numbers, from various areas may then be tested for correlation. As already emphasized, this correlation is not the same as causation, and more precise evidence should therefore be obtained from field experimentation. The fields or forests are divided into plots, and in some the insect is reduced to a very low level by treatment with an insecticide; the differences in damage between the treated and untreated plots can then be compared with their insect populations. Other factors, including weather, will be the same in both plots, so that any correlation is likely to be meaningful. Damage surveys may also serve in the initial phases of a program of work to lay down the population intensity at which a pest reaches its economic-injury level—the level at which control measures are indicated. Accurate determination of this level is basic to any sequential sampling design, or to any integrated control program.

Qualitative and quasi-quantitative estimates of damage obtained rapidly and regularly from a large area, as with the Canadian Forest Insect and Disease Survey, can be useful in indicating long-term changes in a pest's importance, the onset of periodic outbreaks, the success or failure of current control measures, and which pests are of sufficient significance to warrant more-intensive work. When collected over a long period, such data may also allow a more sophisticated analysis from a variety of ecological aspects.

FACTORS INFLUENCING POPULATION SIZE

Surveys can be used as a research tool to investigate the effects of different factors on the size of the pest population. Information about these factors is necessary to give a fully rational basis to a control program.

The simplest approach is similar to that utilized in damage studies, the correlation of insect numbers with a factor, e.g., weather or parasitism. The weaknesses of this method have already been indicated, and whenever possible an attempt should be made to gather life-table-type data; that is, absolute population estimates of at least one stage of the insect, in such a way that, where appropriate, the techniques of Morris or of Varley and Gradwell can be applied for analysis. Morris' techniques may be used on populations in perennial crops or forests where one generation (n) may be expected to have some relationship to the next ($n + 1$). The relationship between log n and log $n + 1$ is then investigated, and the various other factors, e.g., weather and parasitism, are added into the equation for log n, which is then tested to see if it gives a better prediction of log $n + 1$. The factors giving the best prediction are those associated with the major part of the change in numbers from generation to generation and are referred to as the "key factors."

Often, as with annual crops, successive annual generations may have no significant direct biological relationship, but for such crops it may be particularly important to determine the role, if any, of natural controlling factors in influencing the size of the economic population. Put another way, Is natural control having any significant effect that we should try and preserve when planning the use of pesticides? This can be answered by estimating the number of eggs laid and the size of the resulting economic population in a number of different areas or years, or both. The resulting population is plotted against the egg population, and the extent to which variations in egg numbers influence the numbers of the later stage will be shown by the coefficient of determination (r^2). A high value of r^2 will indicate little significant natural control; a low value may indicate very striking changes in numbers after the egg stage, which may be brought about by natural control.

PREDICTION AND THE NEED FOR CONTROL MEASURES

One of the fundamental aims of the entomologist is to be able to predict outbreaks of pests, so that appropriate pesticide treatments may be applied when required, but not otherwise. The survey is the basic method enabling him to do this. In general, some preliminary work is necessary before a prediction survey can be started. This work, outlined previously, should indicate the numbers of insects associated with the economic-injury level and the extent to which subsequent populations can be predicted from previous generations or from egg numbers. The relative roles of natality and mortality are important, as are the reproductive potential of the female adults, which can often be determined from their size or the size of the pupae.

The entomologist's decision to exercise control measures is determined by the numbers per unit of habitat reaching a certain level. Often it is not just the level of the population but the time at which this level is reached that is important, that is, time relative to the development of the crop. Therefore, the statement will be in the form: If the numbers of eggs reach or exceed x per bush before 50% of the flowers have opened, or y per bush after more than 50% of the flowers have opened, control measures should be applied.

The difficulty arises of determining when the population level is truly x. This involves problems of sampling, which are discussed in more detail elsewhere, but one approach is to take a sufficient number of samples to insure that the fiducial limits will lie within 10% of the mean. With very high or very low populations, this method will mean that many more samples are taken than are really needed to be sure that the population level is in excess of x or far below it. This situation can be overcome by the use of sequential sampling, which provides an ideal and efficient plan for a survey. A large amount of initial work is necessary to determine the type of distribution occurring in the field, i.e., whether it is negative binomial, Poisson, or another type, and also the variance–mean relationship. When these statistics are known, and using the equations set out by Morris, Southwood, and others, a sequential sampling chart can be prepared. With these sequential sampling charts on hand, survey operators can immediately read off from each sample taken whether further samples are required or whether control measures should be taken.

METHODS OF SURVEYS

Many methods of assessing insect numbers are available, as already indicated. Some measure absolute population per unit area; others, such as traps, measure only relative numbers. Traps may be influenced by their efficiency and the weather, as well as by numbers of insects present.

In survey work, the first decision concerns the stage of the insect to be sampled. When pest control is the object, the aim should be to provide information sufficiently in advance to allow the control measures to be applied before the damage is done. Therefore, if measures are to be taken against a pest that causes damage as a young larva and has a short developmental period, e.g., the codling moth, it may be necessary to predict from a survey of ovipositing females. When damage is being surveyed, the greatest accuracy will be obtained by counting the damage-causing stage.

ADULTS

More or less absolute estimates of flying adults can be obtained by using the types of suction trap developed by C. G. Johnson and L. R. Taylor. If the traps are exposed to very different wind speeds, a correction needs to be applied, and Taylor has published tables of correction factors.

There are various interception traps that are simpler to construct, but they give results that are more difficult to interpret. Suspended cone nets may be used to trap aphids (and other insects with low flight speeds) in exposed situations, and sticky traps and sticky nets, because of their greater ability to retain the insects, may be used in a wider range of situations. The numbers taken by such traps will be greatly influenced by wind speed and by the flight speed (roughly equivalent to the size) of the insect. Taylor has shown how sticky-trap catches may be corrected to allow for these effects, but it is necessary to have continuous records of wind speed at the site of the trap. Water traps also give records of aerial abundance; like sticky traps, they may be painted various colors, and this will affect the numbers and type of insect caught. Because of the shape of water traps and the resultant wind eddies around them, catches from such traps are less easily corrected for the effect of wind speed than are those from sticky traps. Furthermore, water traps cannot be left unattended for long periods, because the water may evaporate, or, if there is heavy rain, it may overflow. Water traps do, however, have the advantage over sticky traps of preserving the insects in fairly good condition for identification.

Light traps also are widely used to trap adult insects, but they can introduce sources of error; e.g., the chances of capturing a female moth at light may vary with her age, and the efficiency of the trap will vary with the amount of moonlight or other illumination reducing the contrast between the trap and its surroundings.

Some adult insects are attracted to bait, at least at certain times in their lives. Bait traps have been useful in surveys of fruit flies, fruit moths, and house flies, but the attractiveness of the bait can vary with its age, the position of the trap, and the number of insects already in the trap.

Useful measures of colonization and oviposition can be obtained by placing insect-free "trap plants" or parts of plants, e.g., logs, in the field and recording the numbers of adults or eggs, or both, present after a given time. Shelter traps, consisting of pieces of grooved wood held together with screws, may be used for bark-dwelling and other thigmotactic insects or mites. Hibernating or resting insects will enter these traps and give a measure of their abundance.

When trapping adult insects for survey purposes, it is important to remember that although larger catches may be obtained by using a colored trap or including a bait along with visual attraction, "more" may not be "better." The additional biological errors that are introduced can more than outweigh the statistical advantages of larger catches.

Adults of many insects, such as beetles and bugs, may be surveyed by sweeping, beating, and other methods referred to later under Larvae and Pupae.

EGGS

When eggs are laid exposed on the foliage, a count of the number of eggs per leaf or stem provides a reliable, if tedious, measure of abundance; sometimes the eggs may be washed off with gasoline or some other solvent. Eggs in soil may be sampled by the traditional soil-washing methods. Eggs embedded in plant tissue are the most difficult to assess. Attempts to count them by the use of x ray or differential staining have not been very successful, and careful visual examination, often under the microscope, along with the splitting of the stems, is often the only satisfactory method. Therefore, for survey purposes, some stage other than the embedded egg should be used whenever possible.

LARVAE AND PUPAE

These stages are frequently present on the foliage of plants or trees. The traditional and satisfactory method of sampling arboreal larvae is beating, to dislodge the insects onto a tray. Some workers have found it advantageous to have a funnel and a collecting jar attached to the center of the tray, which can be covered with wire netting to prevent the entrance of twigs. The insects can then be rapidly shaken into the collecting jar and their escape prevented. With more-conspicuous, less-agile insects, a plain cloth-covered beating tray is often adequate, the insects being counted directly on the tray. This can be particularly useful in survey work when a sequential sampling program is being followed. Differential falling of the various larval stages, variations in the prevailing weather, and the tendency to sample only the lower branches are possible sources of error with the beating method.

Larvae on forage crops are more difficult to survey. Use of the sweep net is a convenient and easy method, but it samples only those insects on the tops of foliage, and their presence there will be influenced by weather conditions and the time of day. However, with some standardization in this respect, sweeping still provides an easy, although rough, estimate of the abundance of certain insects for survey purposes, which is especially useful for determining the need for control measures. An absolute estimate of the insect population on a forage crop can be obtained by delimiting an area of it and sucking the insects out with a vacuum-cleaner type of apparatus. A very convenient portable backpack model, driven by a gasoline motor, is now available commercially.

Surveys of a number of crop insects involve dissecting the stems or stalks of infested plants and counting the number of larvae and pupae present. This procedure, together with counts of the number of plants infested, has been used for many years over wide areas in the United States to determine the annual abundance of the European corn borer, *Ostrinia nubilalis* (Hübner), in corn and to provide data for estimating damage by the insect.

The population density of relatively immobile or sedentary pests that are fairly abundant, e.g., scale insects, may be measured exactly by counting directly *in situ.*

The immature stages of many insects live in the soil; they may be sampled by sieving (if the insects are rather large), by soil-washing, or by a behavioral extraction method. Behavioral methods can only be used with mobile stages. There are several types of extractors, e.g., dry funnels, wet funnels, and hot-water extractors. The type used will depend on the insect being studied and the soil type.

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CHAPTER 4

Regulatory Control

Preventing the entry and establishment of foreign plant and animal pests in a country or area and the eradication, containment, or suppression of pests established in limited areas are fundamental regulatory control principles.

Early voyagers into newly opened countries brought in many insects that now infest homes, crops, and animals. International commerce accelerated such introductions. For many years, few legal restrictions on the introduction of plant and animal pests were in effect, and, as a result, many of the most important economic insect pests today are of foreign origin.

In 1873, Germany passed the first regulatory measure prohibiting the entry of products that might spread the grape phylloxera, *Phylloxera vitifoliae* (Fitch), from America. The first important regulatory legislation in the United States was passed in 1877, when four states enacted legislation to afford protection against certain pest species. The initial federal law dealing with animal pests was passed by the United States Congress in 1884. In 1905, the Federal Insect Pest Act was passed, enabling the federal government, for the first time, to regulate the importation and interstate movement of articles that might spread insect pests. The Plant Quarantine Act, approved in 1912, authorized the Secretary of Agriculture to enforce necessary regulations to protect the agricultural economy of this country by preventing the introduction of insects and plant diseases from foreign countries. At the same time, provisions were made for the establishment of quarantines to prevent the spread of pests within the United States.

The savings to agriculture that are realized by preventing foreign pests from entering a country are difficult to determine. However, many important pests have been kept out of the United States since the establishment of quarantine procedures, despite the marked expansion in international traffic and the accelerated speed of travel. An example is the injurious durra stalk borer, *Sesamia cretica* Lederer, which has been intercepted many times at United States ports of entry. In a single recent year, 38,461 foreign plant pests were intercepted at United States ports of entry—an average of 1 every 16 minutes. Also, 401,393 lots of prohibited plant material were prevented from entering the United States in a single year. The United Kingdom, through its enforcement of certain restrictions on the importation of apples from the United States, has prevented the artificial introduction of the destructive apple maggot, *Rhagoletis pomonella* (Walsh). These examples demonstrate that regulatory measures are often practical and successful. Even with the enforcement of quarantine procedures, however, some important pests, such as the cereal leaf beetle, *Oulema melanopus* (Linnaeus), and the face fly, *Musca autumnalis* De Geer, have recently been introduced into the United States

The principle of preventing or retarding the spread of newly established pests by domestic regulatory and control measures has been used to protect agricultural crops against insect pests. For example, the Japanese beetle, *Popillia japonica* Newman, has been under continuous regulation in the United States since 1919. Established infestations still do not exist west of the Mississippi River, and they occur only in isolated areas in the southeastern part of the country. The gypsy moth, *Porthetria dispar* (Linnaeus), which attacks many deciduous trees and shrubs, was first found in the United States in 1869. Control and quarantine programs have confined the pest to a few northeastern states, although there are some 100 million acres of forest west to the Mississippi River known to be susceptible to attack. The sheep scab mite, *Psoroptes ovis* (Hering), which once infested 50% of the sheep in the United States, is now confined to a few states in the Midwest.

Domestic quarantines, combined with treatment programs, have eliminated several pests from the United States. Examples of these include the cattle tick, *Boophilus annulatus* (Say); red tick, *Rhipicephalus evertsi* Neumann, from Florida; parlatoria date scale, *Parlatoria blanchardii* (Targioni-Tozzetti), from Arizona and California; Hall scale, *Nilotaspis halli* (Green), from California; Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), from Florida and Texas; and the khapra beetle, *Trogoderma granarium* Everts, from the United States and also from Mexico. Many of the examples used to document and explain the various regulatory control principles are taken from the United States. However, comparable programs are active in most countries of the world.

Although, in the United States, there are now adequate laws to serve as a basis for needed quarantine action and eradication or suppressive treatments, the success of publicly supported programs is materially affected by the knowledge and interest of all concerned. Quarantine officials solicit the cooperation of other state and federal agencies, commercial carriers, and prospective shippers in obtaining compliance with quarantine regulations. A fully informed public will abide by necessary laws; therefore, special emphasis is placed on an adequate public-information program. Obtaining compliance with regulations has largely replaced enforcement based on law alone. The public must also be adequately informed concerning the application of suppressive or eradicative treatments, particularly when aircraft are utilized.

PLANT AND ANIMAL QUARANTINES

PHILOSOPHY OF QUARANTINE ACTION

The purpose of quarantine is to exclude potential pests, to prevent further dissemination of those already present, and to supplement eradication programs. Individual action cannot prevent the introduction and spread of plant and animal pests. Such protection must be provided through the adoption and enforcement of quarantines by government. Quarantines, therefore, have the protection of economy and welfare as their primary objective.

Quarantines applied to commodities at ports of entry are considered to be the first line of defense against the introduction of new pests. Regulations apply to the introduction of pests carried by commercial transportation facilities. Adequate attention must also be given to other avenues of introduction, such as automobiles, privately owned aircraft, and watercraft. Looking to the future, quarantine measures may be needed in space travel.

If a pest organism breaches the first line of defense, quarantines may be enacted to prevent a limited infestation from spreading throughout the ecological limits of the species. Such quarantine action is more effective when supported by control procedures to reduce the pest population.

If the pest is confined to a limited area rather than distributed over a substantial portion of its ecological range, quarantine action is usually applied at the source of infestation. Conversely, if the pest is widely distributed, it may be more practical to apply regulations at the periphery of the infestation or at the noninfested destination of the pest carrier. Under the provisions of a quarantine, procedures are developed to reduce or eliminate the risk of pest spread associated with the movement of potential pest carriers rather than to prohibit the movement. The degree of quarantine action depends on program goals. Fewer restrictions are necessary if the objective is to retard rather than prevent spread.

It is essential that quarantines be constantly studied in order to make changes that may be necessary to attain objectives. They should be revoked when they no longer serve a useful purpose.

BIOLOGICAL BASIS FOR QUARANTINES

Before a quarantine is considered, it must be determined that the pest is of economic importance and that action is warranted. Quarantines directed against specific foreign pests must not be based on their behavior in other lands. Since introduced pests are not usually accompanied by their natural enemies, they may become of major economic importance, even though they were of little or no concern in their native habitat. For this reason, domestic quarantines are sometimes invoked against pests that are not problems in other countries. Adequate protection by quarantine requires that knowledge be available concerning the identification and ecology of insects that are harmful to man, animals, crops, forests, ornamental plants, stored products, and structures throughout the world.

Before a quarantine is invoked, other possible means of dealing with the problem are explored. There also must be reasonable expectation that the quarantine will be successful in preventing the introduction or spread of the pest and that the economic gain will exceed the cost of quarantine enforcement to government agencies and the public.

If a quarantine is adopted, the habits of the pest are more fully explored, articles that may artificially spread the organism are determined, and procedures are developed that will allow the safe movement of articles from regulated areas. Many articles besides hosts must be regulated, since pests may be spread in association with them. When treatments are being developed to eliminate pests associated with regulated articles, consideration is given to the length of time necessary to kill the pest. Some treatments, such as fumigation, render an article immediately free of pest risk, thereby allowing its safe movement at once. A time lapse is required following some treatments before the pest risk is eliminated; when this is necessary, quarantine action must be continued until the treatments become fully effective.

Quarantines are imposed only on areas known to be infested or on those that have been exposed to infestation to such a degree that there is reasonable cause to presume that the area is infested. Constant surveillance is necessary to determine the extent of pest spread. The habits of the pest and its normal expected rate of natural spread are considered when the need for a quarantine is being decided. Continuous surveys are made in areas particularly vulnerable to invasion by specific foreign pests, as, for example, surveys in Florida for the Mediterranean fruit fly.

MECHANICS OF QUARANTINE ACTION FOR NEWLY ESTABLISHED PESTS

When a pest has been located and quarantine action appears desirable, certain procedures are usually followed: (1) The extent of infestation is determined as promptly as possible. (2) A public hearing is held to allow affected individuals and organizations, as well as representatives of noninfested areas, to express their opinions on the proposed quarantine. Emergency action, however, may be taken immediately prior to holding a hearing if such immediate action should be necessary to prevent the rapid spread of a pest. (3) Unless a different decision is made as a result of views expressed at the hearing, a quarantine is invoked. The quarantine specifies the pest, areas to be regulated, articles subject to regulation, and the basis under which pest carriers may be moved within and from regulated areas. Regulated areas include known infestations and a marginal area based on the biology of the pest. (4) The hazard of spread associated with each of the regulated articles is carefully reviewed, and treatments based on research investigations are developed to allow the safe movement of regulated products. With some regulated articles, normal handling may eliminate the risk of artificial spread. Only slight adjustments in the handling procedures for some other articles will ensure a pest-free product.

Exemption from treatment and certification requirements are allowed whenever possible to relieve any restrictions in keeping with good quarantine enforcement. Utilization of the exemption procedure expedites the movement of regulated articles and avoids imposing undue restrictions on industry.

Regulated articles may be moved from infested areas on the basis of the following: (1) approved treatments are applied; (2) inspections are made indicating that the articles were produced in noninfested portions of the regulated area; (3) the articles have been examined and found to be free of the pest; and (4) the articles have been grown, produced, or handled in such a manner that no infestation will be transmitted. Movement may also be permitted if the articles are to be transported to designated processing plants where the pest risk is eliminated through processing, or if they are to be shipped to geographical areas where the pest cannot become established.

In order to seek quarantine compliance, efforts are made to make the regulations known to the affected individuals and industries. Various means are employed to check on quarantine compliance. If the objective is to prevent spread, enforcement may involve the inspection of all types of traffic leaving regulated areas. If the objective is to retard spread, or if the regulated articles can be adequately checked at the source, such drastic action may not be necessary, and only spot checks are made. Regulated articles may also be checked at principal transportation centers, truck-weighing stations, and other similar points.

EXPORT CERTIFICATION

Certification of plant material for export is an important phase of foreign plant-quarantine activities. Phytosanitary laws of foreign countries are translated, summarized, and made available to exporters. Whenever possible, plant material that meets the requirements of the country of destination is certified before it is exported. This procedure is sound and avoids the problems associated with treating infested materials after importation.

LEGAL RESPONSIBILITY

In the United States, the United States Department of Agriculture, under federal laws, has broad authority and responsibility to enforce quarantine regulations to prevent the entry or retard the spread of plant and animal pests, as well as to develop and carry out programs designed to eradicate, control, or suppress such pests. The so-called animal-quarantine legislation is encompassed principally in acts passed in 1884, 1890, 1903, 1905, and 1962. Authority for federal participation in the plant-quarantine field dates back to the Insect Pest Act of 1905 and the Plant Quarantine Act of 1912. Control and quarantine programs have been strengthened by the passage of a number of additional acts and amendments to these initial regulations.

Work conducted under the provisions of these laws includes cooperative activities carried on jointly with state and local governments, other organizations, and individuals. Since suppression and control programs must be handled in accordance with state laws and in cooperation with the states, the programs are effective only where the states concerned have a strong and continuing interest in the particular pest problem.

Active cooperation between many countries in the enforcement of plant quarantines followed a conference called by the Food and Agriculture Organization of the United Nations and the adoption in 1951 of an agreement entitled "International Plant Protection Convention." All major nations now have plant-protection laws and regulations to guard against the introduction of plant pests that could become established under their ecological conditions. For example, the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), was introduced into Germany, and local infestations, discovered in 1874, were eradicated. A decree was issued by the German government in February 1875 forbidding the further importation of potatoes and potato sacks. France also imposed exclusion measures against the same pest in 1875. These two exclusion orders anteceded, by a few years, the Destructive Insects and Pest Act adopted by the United Kingdom in 1877. Many countries regulate the entry of host material that might introduce exotic, economic species of fruit flies.

State agencies are responsible for enforcing quarantine regulations to prevent the spread of pests within a state. They may also enact legislation to prevent the introduction of pests of particular concern to them from either foreign or domestic sources, provided the federal government has not enacted quarantines against the specific pests.

MOVEMENT OF SCIENTIFIC SPECIMENS

Under the provisions of federal and state regulations, approval may be granted to import or move living pests interstate to specific locations for scientific purposes. Such approval is based on a careful review of each case by the state and federal agencies concerned.

It is desirable to conduct scientific studies in areas where the pest is known to occur. If this is not possible, the next choice is an area well removed from those in which the pest could become established if it escaped. If the research must be conducted in areas where the pest is not known to occur and might become established, first consideration is given to determining whether adequate safeguards can be maintained to eliminate any possibility of escape. Other considerations include the type of studies to be made, the potential biotic range of the pest, and its relative importance, as well as the possibility that it may represent a new race or strain that is not present in the area where the investigations are to be conducted. Issuance of a permit depends on this review. It is important that everyone abide by laws regulating the movement of living pests and recognize his responsibilities in preventing escape or illegal transport of the pests.

REGULATORY CONTROL PROGRAMS

Publicly supported regulatory control programs are an essential part of the over-all effort to protect crops and livestock from pests. These programs are based on the results of the best available research information, and research should be continued as long as the programs are operated, so that improvements may be made.

There are three main types of organized publicly supported pest-control programs: eradication, containment, and suppression. Eradication and containment programs also involve regulatory activities to prevent reinfestation or spread to new areas. The type of program to be conducted depends on the objectives.

Various methods are used in eradication, containment, and suppression programs; these include chemical, cultural, and biological measures. Chemical-control procedures for eradication have been effective and economical, but the chemicals must be used in such a way as to cause minimal adverse side effects. An important consideration in the use of toxicants in organized publicly supported programs is the assurance that the materials are applied under the direction of employees trained in the proper application of pesticides. The total amount of chemical required for the control of a pest in programs of this type is usually less than the quantity that would be utilized by the general public should the pest be allowed to spread throughout its ecological range.

Cultural-control procedures are used whenever possible, but they usually cannot be relied on to attain eradication unless combined with other treatments. Over the years, numerous biological-control organisms have been of considerable benefit in containing but not eradicating serious pests. However, there have been a few instances where biological procedures have been responsible for pest elimination. An example is the eradication of the melon fly, *Dacus cucurbitae* Coquillett, from the island of Rota near Guam in the South Pacific by the male-sterilization technique, in which gamma radiation is used. With other pest-control programs, it is possible to utilize cultural and biological procedures in combination with chemical control and attain the desired objective.

ERADICATION

Eradication programs are those conducted for the purpose of eliminating the target organism from a geographical area. Although no plant pest has been eradicated from the entire area where it is known to occur throughout the world, many species have been eradicated from limited geographical areas.

Eradication programs are usually applied against pests that have recently gained entry and are not established over a large portion of their potentially favorable ecological range. If adequate control methods are not known when the pest problem is discovered, even though eradication is desirable, such a program may not be undertaken until new procedures are developed. At times, new technology makes it feasible to eliminate pests even though they are firmly established over a sizable geographical area. An excellent example is the eradication of the screw-worm, *Cochliomyia hominivorax* (Coquerel), from the southeastern United States, which resulted from the application of the sterile-male technique explained in detail in Chapter 15.

Although there may not be sufficient data to develop procedures assuring eradication when a new pest is found, eradication programs may be tried to reduce actual or potential crop losses. For example, white-fringed beetles, *Graphognathus* spp., were seriously damaging crops in southern Alabama and northwestern Florida when first identified; therefore, it was the consensus of state and federal workers and others that every effort should be made to attempt elimination with the tools available. When it was demonstrated that the pest could not be eliminated with known methods, the program objective was changed to one of containment.

Some newly introduced pests cannot be eradicated or contained with any known procedures. An example is the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), which first appeared in New Mexico in 1954. By the end of that year it had moved to 7 additional states, and in 1967 it existed in 36 states – nearly every place where alfalfa is grown commercially in the United States.

Eradication of a pest is difficult and sometimes must be repeated, as in the case of the Mediterranean fruit fly, first found in the United States in central Florida in 1929, after it had spread over a considerable area. An intensive eradication effort against this important fruit and vegetable pest was promptly initiated. It required approximately 18 months and $7 million to eradicate the infestation. The insect was not found again in the United States until 1956. This reinvasion, similarly, was widespread before being detected by a homeowner in Miami, Florida. In the second eradication program, the same length of time was required to eliminate the pest, at a cost of approximately $11 million. Following the 1956 outbreak, an intensive trapping program was initiated to detect new invasions as quickly as possible. A third infestation, found in 1962, was eradicated by the end of 9 months, with an expenditure of $1 million. A fourth invasion was discovered in 1963 and was eradicated at a cost of $300 thousand within 3 months. A fifth invasion was discovered in the Brownsville, Texas–Matamoros, Mexico, area in June 1966. Following eradication treatments, no further specimens were found after a lapse of 44 days, and all quarantine restrictions were removed within 6 months. A malathion poison-bait spray formulation was used to eradicate the 1956, 1962, and 1963 invasions. This demonstrates the value of constant surveillance for foreign pests.

CONTAINMENT

Containment programs against plant or animal pests that have not reached their full ecological limits are conducted when eradication cannot be accomplished, either because the best has become firmly established or because eradicative treatments are not available. For example, when the Japanese beetle was discovered in the United States, sufficient information was not available on control treatments to make eradication practical. Consequently, the beetle has spread over a considerable area. State and federal governments are still conducting a program designed to contain the pest. It is often advisable to expend public and private funds in an effort to retard the spread of a pest rather than allow it to move unimpeded throughout its ecological range.

In containment programs, there is usually no attempt to reduce or eliminate populations throughout the infested areas; control is generally confined to selected portions of infested areas from which the pest may be artificially spread. It also may be practical to apply measures to suppress the population along the periphery of the infested area to retard natural spread. An example is the program to contain the gypsy moth in the United States. Suppressive pesticidal sprays have been applied along the periphery of the infestation to retard natural spread to the south and west. Such treatments have been largely responsible for restricting this pest to a small portion of its potential range within the country.

In some containment programs, the control effort is aimed at reducing populations throughout the infested area, with the hope that a research breakthrough will make eradication practical at a later date. An example is the recent development of effective soil-fumigation procedures in which a mixture of dichloropropenes and dichloropropanes was used against the golden nematode, *Heterodera rostochiensis* Wollenweber. A progressive eradication program against this pest is being conducted in the only known infested area in the United States—on Long Island and in Steuben County, New York. Prior to the development of the fumigation procedures, the golden nematode had been confined to small areas and kept, or contained, at low populations throughout the infested area by utilizing cultural-control measures.

Containment programs are reviewed at frequent intervals to make sure that the objectives are being attained. Control of the Dutch elm disease, *Ceratocystis ulmi* (Buisman) C. Moreau, in the United States, and its associated bark beetle vectors of the causal fungus, is an example of a program turned over to property owners after eradication and containment efforts no longer appeared feasible.

SUPPRESSION

State and federal agencies in the United States also cooperate with private individuals and grower organizations on programs against some pests capable of periodic sudden outbreaks over such wide areas that control cannot be accomplished by individual effort. These pest-control programs are mostly applied against widely distributed plant or animal pests.

Examples of publicly supported suppression programs designed to control populations of pests occurring over extensive areas are those conducted against several species of grasshoppers or locusts; the torsalo or human bot fly, *Dermatobia hominis* (Linnaeus, Jr.); and the Mediterranean fruit fly. In the United States, grasshoppers in the western states are subject to control annually by state and federal agencies with participation by farmers. Cooperative locust-control programs have been conducted in 13 countries in the Near East, South Asia, and Africa; namely, Afghanistan, Ethiopia, India, Iran, Iraq, Jordan, Lebanon, Libya, Morocco, Pakistan, Sudan, Tunisia, and Turkey.

Central American countries and Mexico cooperate in suppression programs conducted against the torsalo and the Mediterranean fruit fly. The work is coordinated through OIRSA (Organismo Internacional Regional de Sanidad Agropecuaria) and is financed by Nicaragua, Guatemala, El Salvador, Costa Rica, Honduras, Panama, and Mexico.

MONITORING THE EFFECT OF CONTROL PROGRAMS ON THE ENVIRONMENT

The pesticide-monitoring responsibility in large-scale control operations may be defined as a surveillance activity designed to assure high operational performance and adherence to safety precautions in the application of substantial amounts of pesticides to areas under treatment. Its goals are maximum protection of public health, the applicators, domestic animals, fish, wildlife, and other organisms.

It is axiomatic that most biological, cultural, or chemical-control procedures applied against a specific pest have some effects on other organisms, referred to as side effects. This is true whether the selected control procedures are applied by rural or urban individuals or by public agencies. The extent of such effects on other organisms is largely dependent on the size of the control operation. Since the initiation of organized pest-control programs, scientists have attempted to utilize procedures that would have the least detrimental side effects. Initially, evaluation of side effects was made principally by research workers who were at the same time determining whether the treatments would be effective for control of the target organism.

Studies on the side effects of heptachlor treatments for the control of the imported fire ant, *Solenopsis saevissima richteri* Forel, in the United States, especially the residue problems associated with food and feed crops and wildlife, brought widespread attention to large-scale use of persistent pesticides. The combination of studies on the impact of the programs conducted against the imported fire ant led to changes in control procedures. A specific insecticide bait was developed that, under the conditions of use, is not hazardous.

Side effects associated with large-scale eradication, containment, or suppression programs can be beneficial. For example, chlorinated hydrocarbon insecticides mixed with agricultural soils for the control of Japanese beetle, white-fringed beetle, or European chafer, *Amphimallon majalis* (Razoumowsky), larvae also provide control of numerous other soil-inhabiting pests, including certain wireworms, rootworms, and root aphids. Fumigation treatments to eradicate the khapra beetle also eliminate other grain-inhabiting insects and rodents. Certain storage-insect pests are controlled as side effects to treatments applied to fields of small grains for cereal leaf beetle control in the United States.

Monitoring assumed a major role in control programs in the United States in May 1963, following release of the President's Science Advisory Committee report on "Use of Pesticides." In the committee's recommendations the subject was referred to directly, as follows: "Provide as a part of the operating budget of federal control and eradication program funds to evaluate the efficiency of programs and their effects on nontarget organisms in the environment. Results of these studies should be published promptly."

Monitoring, from the standpoint of large-scale control programs, is concerned with the gross or immediate impact of a disruption in the environment brought about by direct application of a pesticide. It deals with the acute and more-dramatic effects of a single or a few pesticide applications, on an area a few-hundred to several-thousand acres in size. Results of monitoring investigations may establish or point to the need for research studies on long-term chronic effects of a pesticide program on the biota.

A decision to initiate large-scale plant-pest control or eradication programs is reached after careful consideration of all factors involved. First, the importance of the pest to agriculture or public health must be appraised. Then, all that might be adversely affected by the procedures to be used must be reviewed. When pesticides are employed in the total effort, the following factors must be considered before initiating the program:

1. Effectiveness against the target organism.
2. Possible hazards to applicators and to people residing in treated areas.
3. Residues on food or feed crops.
4. Hazards to fish and wildlife.
5. Danger to the honey bee, *Apis mellifera* Linnaeus, and other pollinators, or possible detrimental upset in the balance of beneficial insect complexes.
6. Effects on soil organisms or on plants grown in the treated soil.
7. Water pollution, with special reference to: endangering public and private water supplies for use by man and domestic animals, including contamination of soil by water used for irrigation; residues in fish and other aquatic organisms; and effect on food-chain organisms.
8. Possible contamination of surrounding areas through air drift or water movement.
9. Possible absorption and translocation of the pesticide by the plants.
10. The mechanism of action and persistence in soils.

The decision to monitor a control program is based on many considerations. The most important are: (1) the type of pesticide to be used; (2) the type and size of the area to be treated; (3) residues already in the environment; and (4) possible hazard to plant and animal life in the area.

SUPPORTING ROLE OF RESEARCH AND METHODS IMPROVEMENT

Control and quarantine programs usually involve pests of foreign origin that have been recently introduced. Consequently, research data for developing control and regulatory measures may not be available. Even when there is basic laboratory-research information about the particular pest, the adaptation of these data to large-scale quarantine or control operations requires considerable expansion and field evaluation. Basic-research accomplishments must be rapidly transposed into workable action programs.

Several special-methods improvement laboratories have been established in the United States. The laboratories are staffed by personnel who work in close collaboration with other research scientists to develop practical regulatory and control procedures.

An example of cooperative research and methods improvement illustrates the value of this type of approach and how it can be used to minimize or eliminate some of the adverse side effects associated with large-scale suppression programs. During the early stages of the imported fire ant program in the United States, a single application of heptachlor, a chlorinated hydrocarbon insecticide, was the only known means to control the ants effectively. However, there were adverse effects of the insecticide on fish and wildlife. A program to develop alternate control procedures was accelerated, and intensive screening of materials led to the development of a bait formulation consisting of soybean oil, corncob grits, and a minute quantity of the insecticide mirex. When this bait is applied at the recommended rate, only 1/7 oz of the insecticide is distributed per acre. The bait has no adverse effect on fish and wildlife and does not create harmful residues. The development of this formulation made it possible to continue the large-scale suppression operation.

A significant advance in the field of chemical pest control through methods improvement was the development of the ultra-low-volume-treatment technique. This involves the application of minute quantities of undiluted or highly concentrated technical insecticide. Some chemicals applied in this manner, even at a reduced per-acre dosage, control pests more effectively than when applied in a diluted form. Application costs are lowered because of the increased acreage that can be treated per application unit, particularly when aircraft are utilized. There are also savings in costs associated with mixing and transporting the chemicals. Since the need for mixing is eliminated, there is a reduction in the hazard involved in handling the toxicants; and in aircraft application there is greater safety to the pilot, since the material may be applied at a higher flight level. The low-volume-treatment technique has been used effectively in publicly supported suppressive programs in the United States against pests such as grasshoppers; the boll weevil, *Anthonomus grandis* Boheman; and the cereal leaf beetle.

Although the goal of pest-control programs is to develop an effective treatment entirely free of objectionable side effects, this is seldom possible. There are exceptions, however—notably the eradication of the screw-worm fly in the southeastern United States through the release of sterile insects of this species. The elimination of the screw-worm from the southeast has been of untold benefit to the livestock industry, and there have been no complaints from farmers about the eradication method used. In addition, increases in deer populations have occurred in the area, and this has been commented on favorably by those interested in wildlife. The sterility principle also shows considerable promise against certain fruit fly species and is being investigated as a means of controlling other important plant and animal pests.

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CHAPTER 5

Ecological Basis for Control

Since the late 1940's, many workers concerned with the control of crop pests in North America and elsewhere have strongly advocated a more fundamental approach to pest-control problems. The limitations of chemical control were recognized, as well as the fact that control measures could not be significantly improved without ecological knowledge of the species to be controlled. As a consequence, much-needed emphasis has been placed on ecological studies basic to an understanding of the causes of pest outbreaks and of the requirements for long-term control of the pests. Discussed in this chapter are (1) the special nature of crop ecosystems (agroecosystems) in which pest outbreaks develop, (2) special attributes of pest populations at or near epidemic levels–levels that normally warrant control, (3) the biometrical techniques required to measure pest-population parameters, and (4) the practical and scientific application of results of long-term studies on the dynamics of insect-pest populations in agricultural ecosystems.

THE ECOLOGICAL APPROACH

The study of a pest population in a crop ecosystem, in relation to chemical, biological, cultural, physical, or integrated control practices, must be considered in a study of fundamental relationships among host plant, pest population, and related biotic agents, soil, climate, and the management practices of man. Soils, host plants, and management practices, singly or combined, are relatively stable in the maintenance of crop stands in full production, but pest populations and related natural control factors–parasites, predators, diseases, and weather—fluctuate dynamically from time to time and clearly contain clues to pest-population increases and decreases. An exception may be the distribution of an insect-resistant crop variety such as wheat resistant to the Hessian fly, *Mayetiola destructor* (Say) (see Chapter 6). Insight into the primary causes of pest outbreaks can therefore be gained through detailed studies of extrinsic and intrinsic factors acting on the pest during the rise and fall of local or widespread infestations. Such a study must be long-term, so that exact relationships between mortality factors and host population within and between generations can be elucidated. This approach may ultimately provide growers with a practical means of pest control and science with a fundamental explanation of the underlying biological phenomena.

AGROECOSYSTEMS

Ecosystems are self-sufficient habitats where living organisms and the nonliving environment interact to exchange energy and matter in a continuing cycle. Descriptions of such systems have varied slightly in the past only because of the different conceptions of the systems' space and time limits, the components involved, and the various approaches taken in their study.

Agroecosystems, or crop systems, are special situations; variations here are caused mainly by the nature of the crop environment, the host plants and arthropod species that are present, space and time boundaries, and the distribution of a species in a crop area during the rise and fall of a local epidemic. These systems are relatively artificial but stable in nature. Homogeneity of crop conditions causes the artificiality, while regularity and uniformity of management practices create stability. The host plant and soil-substrate components may sometimes limit the development of pest populations, and some mortality factors, extrinsic and intrinsic to the populations, can limit pest numbers from time to time.

Agroecosystems usually contain a few common or major species and numerous relatively rare or minor species. In apple orchards, for example, the ratio of major to minor species is approximately 6:150. In any outbreak, usually only one pest species, most often a major species, is present in high densities, and the other species are relegated to such low numbers that they cannot be effectively sampled. Consequently, the study of a pest outbreak in an agroecosystem is in reality the study of one pest species in relation to natural control factors, or in relation to man-made factors superimposed on natural control factors, and this constitutes a study of the variable components of the system under these conditions. Such a system is a much simpler study situation than is frequently envisaged, and it is ideally suited to the population-dynamics approach.

PEST POPULATIONS

Because, in the control of crop pests, concern is chiefly with the species as it behaves at the population level, this is the level at which to seek solutions to pest-control problems. Pest populations are composed of groups of individuals, in one or more stages, of a single species; the groups occupy a particular habitat and have characteristics peculiar to the group rather than to the individual. Major population characteristics, such as density, birth and death rates, age distribution, biotic potential, and growth, are biological attributes of the population as a whole and are meaningful only because the life stages of the population—the egg, larva, pupa, and adult—are interdependent and interrelated. Because these stages are the dynamic units of the population, and collectively have definite organization and structure, they can be described and expressed as statistical functions. Thus, to obtain fundamental information on the population dynamics of a species, it must be realized that individuals in one stage are not isolated from individuals in other stages and that they cannot survive independently of the population; in other words, there is no sharp break between any two stages in a population. Therefore, eradication of a pest by controlling only the damaging stage is difficult, because some of the individuals usually survive to assure continuity of the species.

Control studies have often been short-term and concerned mainly with the damaging stage of a pest population, usually the larval stage, and entomologists have therefore become accustomed to think of the stage and not the population as the ultimate unit in pest control. But it is necessary to know not only what effect chemicals, parasites, predators, resistant crop varieties, and any other control measures, singly or combined, have on a given stage, or even on a limited number of stages of a pest population, but also the effect of each on all stages and indirectly on population trend. However effective a factor may be against a given stage of a pest species, its value is limited if it does not account for significant decreases between generations. To know that a factor kills 95% of the eggs or larvae of a pest tells little if the extent of the effect of such a factor on population regulation is not known.

POPULATION MEASUREMENT

A study of the primary causes of pest outbreaks includes the measurement of population changes from generation to generation and the study of the factors responsible for these changes. A quantitative approach to such studies is now possible through the use of recently developed sophisticated sampling techniques that provide for the collection of data of the required quantity and quality. Multivariate statistical techniques can be used for the analysis of the action and interaction of the many population parameters that are measured, and systems analysis and allied computer techniques permit realistic and precise analyses of whole systems and not just fragments of them. These techniques are specifically suited to handle both the magnitude and kind of complexity found in agroecosystems. Their use should provide the key to a precise understanding of these ecosystems and to the intelligent and practical manipulation, for control, of mortality factors or husbandry practices in crop habitats. In pest-population studies, the first concern is with the interaction of pest stages and their mortality factors within and between generations. For knowledge of this, a population-dynamics study has priority and is basic to the correct interpretations of the action of mortality factors, singly or combined, in the population regulation of the species. Specifically, basic requirements for the adequate measurement of the parameters involved are (1) that confidence limits be biometrically established for all population data collected; (2) that all stages of the pest population, and related mortality factors, be measured and appraised in terms of a common unit; and (3) that such data be collected for several generations of a species, during the rise and fall of an infestation.

To analyze collected data, and to determine their long-term population significance, a series of life tables should be prepared. The life table is a useful numerical aid or device used in the study of insect populations to record in a systematic fashion those facts basic to the age distribution of mortality. Conventionally, it consists of data and calculations arranged in a series of columns, from left to right, under the following symbols:

x – the age interval. Convenience usually dictates that these intervals correspond to development stages of the insect.
1_x – the number alive (1) at the beginning of the age interval noted in the x column.
d_xF – the factor (F) responsible for the death of individuals (d_x) within each age interval.
d_x – the number dying (d) within the age interval stated in the x column.
$100q_x$ – percentage mortality (d_x as a percentage of 1_x).
$100d_x/N_1$ – the percentage of generation mortality (d_x as a percentage of N_1).
N_1 – the number of eggs observed in the present generation.
N_2 – the number of eggs observed in the next generation.

An example of a life table for one generation of the eye-spotted bud moth, *Spilonota ocellana* (Denis & Schiffermüller), on apple in Quebec, is illustrated below:

x	1_x	d_xF	d_x	$100q_x$	$100d_x/N_1$
Eggs (N_1)	100	Parasites	30	30	30
		Predators	10	10	10
Larvae	60	Frost	55	92	55
Pupae	5	Parasites	3	60	3
Adults	2	(Sex ratio = 50:50; $\bar{x}$ eggs per ♀ = 100)			
Eggs (N_2)	100				

$$\text{Population trend (index)} = \frac{100\ N_2}{100\ N_1} = 1$$

Index:
Unity = population constant
>1 = population increase
<1 = population decrease

From these tables may be determined: (1) the initial density and survival rate within each stage of the pest population, (2) the mortality factors present in each stage and their effect, and (3) the survival rate after application of insecticide to each stage. More important, from such a series it is possible to determine biometrically the stage and the factors in the stage that are most responsible for the increases and decreases in pest numbers between and within generations and that warrant further experimental and field investigation.

A population-dynamics study also reveals information of immediate practical value: emergence dates and duration of economically important stages, of use in chemical control; the degree of crop injury in proportion to pest density, of use to the grower; and forecasts of densities of pest populations, based on the index of population trend, of use to the grower in planning spray programs.

Finally, this approach to the measurement of pest-population parameters should result in equations that describe observed data. The use of such equations, rather than those that presume certain modes of action, offers the best hope of expanding an understanding of animal processes. Simply stated, such equations are predictive equations in which the dependent variable may be population density N at some future time $t + 1$, and the independent variables are density at an earlier time t, along with weather, predation, parasitism, diseases, and other factors that determine the rate of change in the population between t and $t + 1$.

MULTIFACTOR STUDIES

Detailed studies carried out from 1953 to 1968 on the population dynamics of 11 Canadian crop insects have provided basic information for the practical application of ecological principles in the management and control of the pests. Some of these studies covered as many as 18 generations of the pest species. Sequential measurements were made of the stages and mortality factors in each generation of the pest and were transferred to life tables. For each generation, the estimated numbers of eggs, larvae, pupae, and adults were obtained by measurements made under natural conditions, that is, in crop fields untreated with insecticide. All estimates were based on a standard sample unit and conformed to predetermined confidence limits. Rates of predation, kills by weather and other factors, and percentages of parasitism were derived from frequent field observations or from extensive rearings of host material. Sex ratio of adults was obtained from the pupae, and degree of fecundity was obtained from adults reared under field conditions in the absence of natural mortality factors. Adult mortality was based on an indirect measurement representing the difference between the initial egg population observed in the field and the number of eggs expected on the basis of egg potential of adults of the previous generation. A population increase, decrease, or equilibrium was measured, as illustrated previously, as the number of eggs laid in one generation divided by the number laid in the preceding generation.

When a sufficient number of life tables, replicated in time and space, had been compiled for a species, a simple correlation analysis was carried out to show which stage (critical age interval), and which factor (key factor) within that stage, contributed most variation to population trend. Species studied were as follows:

Species	Origin	Generations Studied	Critical Age Intervals	Key Factors[a]
Fruit-tree leaf roller, *Archips argyrospilus* (Walker)	North America	6	Pupa, adult	Parasitism, migration
Diamondback moth, *Plutella maculipennis* (Curtis)	Europe	18	Adult	Weather
Imported cabbageworm, *Pieris rapae* (Linnaeus)	Europe	18	Larva	Disease
Pistol casebearer, *Coleophoro malivorella* (Riley)	North America	7	Larva	Parasitism
Eye-spotted bud moth, *Spilonota ocellana* (Denis & Schiffermüller)	North America	7	Larva	Weather
European corn borer, *Ostrinia nubilalis* (Hübner)	Europe	5	Adult	Migration
Colorado potato beetle, *Leptinotarsa decemlineata* (Say)	North America	6	Larva	Food supply

Species	Origin	Generations Studied	Critical Age Intervals	Key Factors[a]
Winter moth, *Operophtera brumata* (Linnaeus)	Europe	8	Pupa	Parasitism
Oystershell scale, *Lepidosaphes ulmi* (Linnaeus)	Europe	3	Egg, adult	Predation, parasitism
Apple leaf miner, *Lithocolletis blancardella* (Fabricius)	Europe	3	Pupa, adult	Predation, weather
Birch leaf miner, *Fenusa pusilla* (Lepeletier)	Europe	9	Larva, adult	Predation, migration

[a] All the factors except weather are density-dependent; weather is density-independent.

KEY REGULATING FACTORS

Analyses of life tables for the species listed showed that the critical age interval could occur in any stage of development and that only one or two key mortality factors (or agents) within the critical stage accounted for regulation, or changes in population trend. These factors varied from generation to generation; this accounts in part for their importance as population regulators. Mortality factors other than those in the critical age interval were low and constant and did not contribute significantly to population changes.

Key factors that affected eggs and larvae in six of the species were of twofold importance: they regulated the population, and they accounted for high kills before or during economically important stages. Key factors in the adult stages of five of the species varied and caused lower mortalities, yet their effect on population regulation was just as great.

In 9 of the 11 species studied, the key factors were density-dependent and therefore regulatory; that is, they acted severely against the population when pest density was high, and less severely when density was low. Results confirmed what had been expected: as a rule, biotic factors were density-dependent and physical factors were density-independent.

The population of each species increased and decreased at the same time in all areas of the species' range. For instance, the eye-spotted bud moth was equally abundant in southwestern Quebec and 300 miles east (Iles aux Coudres), and was then reduced by frost (-29°C) in both areas at the same time. The life tables of this species showed only this key factor. Hence, frost apparently regulates populations of this species in all major apple regions of Quebec.

The implication of such findings is that, if the successful manipulation of key factors for population regulation is subsequently made possible through sound studies of the components involved, the results would have very broad application.

Findings regarding crop-plant insects could be considerably modified, the extent of modification depending on the resistance (including tolerance) of the crop varieties on which the insects are feeding. Resistance is especially well-studied in the European corn borer, *Ostrinia nubilalis* (Hübner), where larval population reductions in excess of 60% have often been recorded on resistant compared with susceptible varieties in the same tests. Resistant varieties can also have extensive effects on insect and protozoan parasites and have influenced efficacy of chemical control where such relationships have been studied. Therefore, the ecological interrelationships of crop varieties, which can be changed yearly by the grower, can be extensive.

Biotic

Population densities of 7 of the 11 pests were regulated by insect parasites, predators, or diseases. The number of hosts attacked by parasites or predators depended not only on host density, but also on the density of the agent and frequency of attack. Thus, where these key biotic agents are removed by pesticides, an upsurge in the pest population occurs. By simulating responses involved in predation, it was shown that the number of prey consumed depended on prey density, rate of discovery, hunger level, and time spent by the predator in consuming prey. Similarly, a functional response was implicit in the investigations of all 7 species.

Since none of the parasites or predators regulating the populations of these pests had been introduced to control them, it is apparent that under certain circumstances resident biotic agents can effectively control major crop pests. The winter moth and birch leaf miner are recent introductions to Canada. Considerable resistance to their establishment in that country was offered by resident parasites and predators: mortalities of 98 percent or less in a generation at first permitted some population increase, but higher mortalities subsequently reduced populations.

In-depth studies of the components involved in the manipulation of these beneficial biotic agents are a logical next step, because the importance of these species in the suppression of pests cannot be questioned.

A capsule virus, i.e., a granulosis virus encapsulated in a crystalline container, was the key factor that suppressed field populations of the imported cabbageworm. The death rate from the disease caused by the virus was an increasing function of host density. The practical application of this information is under study in control of the cabbageworm in large crop areas of southwestern Ontario. Disease-producing organisms such as this virus are usually density-dependent, because the denser the population of the host, the more easily transmission from environment or from diseased insects to healthy ones occurs, and in dense populations the microorganisms are able to increase at a more rapid rate and in greater numbers than do the host insects.

Abiotic

Weather was a key factor in two of the species studied, and food supply in one. Weather is a key mortality factor independent of density. Under its favorable influence during several seasons, or, in the case of multivoltine species, during a single season, a pest may build up to outbreak numbers and fluctuate at epidemic levels. Thus, in a local situation, for instance, near the distributional limits of a species, climatic factors may obscure the action of density-dependent agents that operate concurrently but at a lower level of mortality. These agents may well be regulative in more-typical parts of the range. As an example, in eastern Canada the diamondback moth survives only in the spring and summer and fluctuates in numbers according to the type of weather that prevails during the flight period; in South Africa, its numbers appear to be regulated by density-dependent factors throughout the year, because the weather there is rarely adverse. A much different situation prevails for the bud moth: frost regulates the species over long periods and over large areas. In relation to regulating factors, it should be pointed out that the simple categorizing of factors as density-dependent or density-independent does not *per se* determine the effect of a key factor on population trend, but rather it is how sensitive the pest is to variations in the key factor that is important. In the case of the bud moth, the further very important action of frost in selection of frost-resistant strains of the species, and thus on subsequent density of the pest, cannot be discounted.

In field populations of the Colorado potato beetle at Ottawa, Canada, intraspecific competition for food was the key factor. Mortality agents are few in potato fields, and in most years the available food supply governs the number of progeny reaching adulthood. Upon depletion of the food, the partly fed larvae simply starve or, having limited powers of dispersal, wander about ineffectually until they die.

Migration

Migration was a key mortality factor in three of the species studied and generally resulted from overcrowding; that is, it was density-dependent. Migrating insects successfully re-established themselves only in new areas where food sources and breeding conditions were suitable; heavy mortality occurred where food was scarce or inferior. At high population densities, foliage-feeders may decrease their food supply with time, so that food becomes scarce when the heaviest feeding occurs and most of the reproductive material is being laid down in the insect's body. A proportionately greater reduction in egg substrate and a corresponding decrease in the egg load may follow. This increases the ability of females to fly and the distance they travel. Maximum egg loads are developed at low population densities, and females are forced to lay their eggs in feeding areas. Apparently, this type of migration is essentially a homeostatic response that, in the case of crop species, adjusts the pest population in advance to the capacity of the crop habitat.

Insecticides applied to control the injurious stage of the pest can have no real effect on the total population if they are not applied in areas from which the insect has migrated. Otherwise, control may be more efficient if based on naturally spreading pathogens directed against the larvae, or on the release of sterile males or sex attractants directed against adults.

POSSIBLE REGULATING FACTORS

Other mortality factors may be of significance in population regulation; they act in a density-dependent manner against certain crop pests but have not yet been shown to play a critical role.

Vigor

An example of the action of increased population density on insect vigor is that of the western tent caterpillar, *Malacosoma pluviale* (Dyar). In a favorable environment, the colonial habits of the larvae promote survival of the weaker individuals, because the stronger adults migrate as usual while the weaker individuals remain and oviposit nearby. Thus, progressively weaker colonies are produced locally by an increasingly sluggish resident population, and their numbers swell to the point where they far outnumber the few stronger colonies that remain. Ultimately, the colonies become too sluggish to reproduce and are suddenly eliminated by the first season of inclement weather. Colonies of intermediate vigor are also lost, because their weaker members succumb and those that remain are not sufficiently numerous to provide the silk and mass of insulating bodies required for survival in the now more rigorous environment. The disappearance of the less viable colonies from the population increases the relative number of active colonies. The resulting improvement in population quality leads to an increase in density and thus completes the cycle. The action of vigor in this way suggests population regulation by a homeostatic device that manifests itself in the absence of extrinsic mortality factors.

Fecundity

The influence of population density on fecundity was shown to be significant in spruce budworm, *Choristoneura fumiferana* (Clemens), populations. Below a certain population pressure, maturing larvae fed solely on the current year's foliage of the host tree, but at higher densities they were forced to feed on old foliage, which caused undernourishment of late-instar larvae and a marked reduction in fecundity of the adults. Therefore, reduced fecundity was an increasing function of population density. Fecundity is greatly influenced by crop varieties on which insects feed. When a crop variety is insect-resistant, known effects on insects range in various examples from a very slight effect to entire suppression of the production of young or eggs.

Behavior

In some grasshoppers, the interaction between individuals of a species leads to the emigration of part of the population. The change from the solitary to the gregarious form is apparently initiated by encounters between individuals, and the encounters are more frequent as the size of the population increases. Repeated encounters are habit-forming, and individuals learn to aggregate. Gregarious nymphs are more active and excitable than solitary nymphs, and the wings of gregarious adults are stronger. When the gregarious tendency has intensified to the point where ever-enlarging assemblies of these forms occur, whole swarms take off in a sustained migratory flight. The remaining population then reverts to the solitary nonmigratory phase.

Similarly, self-adjustment of numbers is obvious in highly evolved social insects such as the termites, wasps, bees, and ants. The queen alone is responsible for reproduction and regulates her oviposition according to the quantity and quality of the food she receives and the density of the colony. If crowding occurs, population balance is restored by egg-eating, fratricide, or expulsion of supernumerary members.

Competition

Laboratory studies of the cabbage looper, *Trichoplusia ni* (Hübner), showed that stress of competition for food and space in a crowded environment has a deterrent effect on population growth. Larvae of the looper have preferred feeding sites and are habitually aggressive. Stress of competing for limited feeding space led to reduced food consumption, sporadic feeding, excessive dissipation of energy, and eventually to increased susceptibility to disease. Larvae often died from infection that normally would be nonfatal.

Genetic Factors

Too little is known of the effect of genetic factors in the insect on population regulation. To what extent do such factors cause mortality? There is no doubt that susceptibility of a species to mortality factors is related in some degree to the number of individuals with poor genotypes within that species. A poor genetic constitution, for example, one that lacks somatic vigor or viability, may be expressed in many ways. For instance, eggs are too few in number, of too low viability, or too exposed to predators; a weak larva falls from a branch and is killed; a slow-moving caterpillar is overtaken by a predator; or a mature larva, like that of the eye-spotted bud moth, fails to build a sufficiently protective shelter on apple and is killed by frost. Genetic drift or Sewell Wright effect also is certainly a factor in insects such as grasshoppers, in which the population may contract for a period into restricted colonies. These adverse situations increase the susceptibility of a species to elimination. However, strongly elusive individuals with a high reproductive capacity, and efficiency, have the opposite effect, that is, population survival within the generation and possible population increase from generation to generation.

Furthermore, variability, the outward evidence of a large gene pool, is also evidence of possible genetic change, and change is inherent in population dynamics. The selective presence of key factors is therefore directly or indirectly connected with the genetics of a species and thus with population change.

USE OF MATHEMATICAL MODELS

Rapid progress in the physical and chemical sciences has been brought about by an intimate feedback between theory and adequate mathematical models based on experiment and measurement. If the science of ecology is to become more than merely descriptive, or at best correlational, similar methods must be used; and mathematical models, based on sound multifactor studies of the type reported in this chapter, must be developed for natural insect populations. The time is past when purely theoretical deductions can further the understanding of natural populations, when qualitative conclusions about natural populations are sufficient, and when disconnected bits of information, however quantitative, about the effects of a factor on a population can be accepted as an understanding of that population in the absence of data on other factors and their interaction. The quantification of all population parameters for pest species is needed, since without mathematics we can scarcely begin to think about entities that have more than a few variables. Mathematics provides a quantitative description of events that occur during the rise and fall of a pest population and permits a calculation of the consequences of purposeful alterations of certain population parameters. Thus, there are two main reasons for the study of natural populations of crop pests by the use of life tables and mathematical models: the desire of the economic entomologist to learn how to manage pest populations on a scientific and optimum rather than on an *ad hoc* basis; and the desire of the population theorist to gain field data to test his theories and to bring to them the new conceptual strength that is possible only through the integration of theory and data.

Mathematical models are really mathematical statements that make biological sense, that attempt to mimic numerical changes taking place in natural populations, and by which quantitative predictions can be made. Such models, based on life-table data and key-factor information, will be used to predict pest-population density at least one generation in advance. This information will be extremely helpful in deciding the necessity for control and in the planning, if necessary, of the logistics of large and often complex operations involved in the application of insecticides or the utilization of the sterile-male technique. The comparison of observed population density or survival rate of an insect pest with the values predicted by a model makes possible the calculation of the proportion of variance in the system that is explained by the model. This is the only scientific method of demonstrating how much or how little is understood about the population dynamics of a species. Explanations of population behavior, stress, vigor, and other factors that fail to show how the models for these factors fit the observed facts, and the degree of predictability achieved, are unacceptable.

Models will also be used to assess the form and degree of interaction by mortality factors within and between stages of a pest species, and their effect on population trend. Mathematical models based on field populations, and developed by multiple regression techniques, provide estimates of these interactions and the variance that interaction contributes. Under controlled conditions, where individual variables are studied separately, interactions cannot be measured.

A third use for such models will be to calculate and test optimum tactics and strategy for pest management. As adequate models become available, many approaches should be possible, within mathematical constraints dictated by economics, that would permit the manipulation of key factors regulating population change. For example, it should be possible to lower the mean population density of a pest and reduce the frequency with which it escapes control by natural enemies or threatens its food supply; to determine when applied control measures are necessary and what control will interfere the least with natural enemies and other species; to determine weak spots in the life cycle of a pest or suggest new methods of control; and to integrate into an optimum form of population management all factors and practices that can be manipulated for pest control. Finally, if dependent or independent variables well correlated with population changes are known, increased insight into the operation of the components of such factors can be obtained in the laboratory, where models can be refined from a descriptive to a more explanatory basis.

The feedback now established between computer and theory is proving to be most effective in the development of models that will become more and more descriptive. All ecologists agree that present models are only refined deductive models and are therefore subject to the same criticisms. However, if the limitations are recognized, the deductive–inductive approach to the building of models should be effective in suggesting unsuspected relations of pest-population parameters that warrant further experimental and field investigation.

PRACTICAL APPLICATION

Results of ecological studies on crop-pest populations have practical application in: (1) The prediction of the population level of each pest from generation to generation. This information, based on trend index data, helps to guide the growers in effective advance planning of spray programs and in more intelligent use of pest-control measures. (2) The feedback of information on the economic thresholds of a pest and on the crop damage caused by the active immature stage. For example, it is now known that five bud moth larvae, or fewer, per 100 leaf clusters on apple do not constitute an economically important population. Hence, sprays are omitted at these densities of the insect, because foliage or fruit damage is below the 5% economic level generally tolerated by the industry. In the spring, chemical control of the bud moth is omitted if winter lows have been -21°F or below, because such lows kill 90 to 95% of the overwintering larvae. However, these lows scarcely affect larvae of the pistol casebearer, which overwinter near the bud moth and receive similar protection, and the omitting of spray applications against the bud moth favors the survival of parasites that control and regulate populations of the casebearer. (3) The utilization of information gained through ecological studies to govern, when possible, the use of insecticides as a possible substitute for other density-independent control factors, such as weather, in integrated pest management practices.

The use of a resistant variety instead of insecticides can often achieve the same results, with obvious advantages. With even a low level of resistance, the persistent and cumulative effect can give control when combined with other ecological factors. The substitution of a tolerant for a susceptible variety can permit increase in parasites, with decreased economic level of damage. The complex interrelationships will require investigations in each specific case.

For the elimination of risks inherent in agricultural pursuits, crop-pest control measures must be integrated according to scientific ecological principles. Pest-control technology has become too complex for reliance on *ad hoc* emergency measures. In the future, not only will entomologists need to provide quantitative data on key factors, important in the dynamics of pest species and their control, but other workers, such as pesticide chemists, economists, and mathematicians, who are also charged with responsibilities in the development of pest-control measures, will have to provide equally detailed field data. On the basis of all the data, stored in computers for the service of growers, it will be possible to determine, with confidence, interrelationships of key factors from all sources involved in the management of crop-pest species. Thus, the integration of all components important in pest-control programs will provide the accurate prediction of pest outbreaks, time, kind, and intensity; the economic threshold levels tolerable for each crop pest; the type of pesticide, virus, bacterium, or other control needed to keep pests at, or below, economic-threshold levels; the required dosage levels of chemicals or pathogens used, and the number and timing of applications; and the most suitable harvest date for crops, as determined by the rate of breakdown of pesticides in or on plants or in the soil.

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CHAPTER 6

Plant and Animal Resistance to Insects

The principle of host resistance in control and management programs involving pests of plants or animals should be given consideration. It should be taken into account in breeding programs aimed at improving the quality or yield of agricultural crops or livestock and in introducing known crop varieties or animal breeds into new geographic areas. Exploitation of resistance to its full potential involves a broad interdisciplinary approach. With a few conspicuous exceptions, consideration has not been given to host resistance in past entomological research.

In recent years there has been some increase in studies of insect resistance in plants, both in respect to the number of plants and insects investigated and to the depth of the studies. There have also been improvements in knowledge of insect physiology and behavior, together with means of studying the minute quantities of various substances that are probably the basis of resistance. For these reasons, some of today's concepts about resistance may soon require modification or replacement. Breeds or lines of cattle, sheep, hogs, and horses possess different degrees of resistance to arthropod attack. This difference in resistance among animals is present from birth to old age and does not depend on previous exposure to the pests.

HISTORY AND EXAMPLES

The ease of insect-pest control by the use of insecticides, at least since 1940, has often resulted in the neglect of a study of host resistance to the pests. This was true even before the widespread use of DDT and other organic insecticides. For example, the satisfactory control of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), obtained with the early arsenicals, apparently made any real, detailed study of the biology of this insect in the United States less necessary, particularly the relation of the insect to its hosts.

In no respect has the study or use of resistance to arthropod pests in domestic animals advanced as far as with domesticated plants. This is partly because of the negligible cost of plants compared with animals, the far shorter time usually required for a generation in plants, and because of greater opposition to hybridization between animal breeds compared with the crossing of plant varieties. In many instances, the findings in studies of resistance to insects, mites, and ticks in animals are similar to principles developed in studies of insect resistance in plants. Most differences are related to mobility of animals, the presence of a blood system and immune reactions, and complexities introduced by the wider role of hormones in animals.

The first instances of the use of plant resistance to insects are as old as the earliest work in applied entomology. The earliest record of a recognizable insect-resistant variety is the Winter Majetin variety of the apple, *Malus pumila* Miller, which was reported resistant to the woolly apple aphid, *Eriosoma lanigerum* (Hausmann), in 1831 and is still resistant at the latest report. Within a few years after the introduction of the Hessian fly, *Mayetiola destructor* (Say), into the United States, an unnamed resistant variety of wheat, *Triticum aestivum* Linnaeus, was mentioned in 1785 by an unknown writer in a farm paper. All trace of some of the first varieties reported as resistant to the Hessian fly has apparently been lost, but, in a few cases, selections of wheat bearing the same names were later found to be resistant. In 1878 it was reported that there was a great difference in susceptibility to grasshoppers, *Melanoplus* spp., in corn, *Zea mays* Linnaeus (Figure 2), as compared with that in sorghums, *Sorghum vulgare* (Persoon). The corn was much more susceptible than the sorghums. Since then, this difference has been seen repeatedly during each grasshopper outbreak in areas in North America where these crops are grown. This is true for all species of grasshoppers that have been observed in outbreak numbers in the area, despite the fact that, during the intervening years to the present, the resistant sorghums have increased from a few thousand acres to many millions, and grasshoppers have not yet "learned" to eat the sorghums. About the middle of the nineteenth century, it was found that some of the American species of grapes, *Vitis* spp., were highly resistant to the grape phylloxera, *Phylloxera vitifoliae* (Fitch), and the European species, *Vitis vinifera* Linnaeus, was very susceptible. This knowledge made possible the grafting of European grapevines onto phylloxera-resistant rootstocks from the United States and formed the basis for a method of control that is still most important. These examples, which are about a century old, and as old as or older than any other insect-control method, emphasize the relative permanence of resistance.

FIGURE 2 Differences in damage to adjacent corn hybrids by grasshoppers, *Melanoplus* spp. *Left*: Kansas hybrid 2234. *Right*: U.S. hybrid 35. Resistance to grasshoppers occurs more commonly in corn inbreds derived from varieties formerly grown in the western United States, where grasshoppers have long been a feature of the environment, than from those in more eastern parts of the country. (Courtesy of Kansas Agricultural Experiment Station)

The first extensive search for sources of plant resistance to insects was made in California over a period of 10 years, beginning in 1881. Seeds of over a hundred varieties of small grains, especially wheat, were obtained, and plants grown from these seeds were exposed to infestation by the Hessian fly. The results were recorded, but nothing further was done for several decades, when development of knowledge of plant-breeding made possible the practical use of the information in incorporating genetic factors for resistance into a satisfactory wheat variety. Possibly the earliest studies of the inheritance of pest resistance were in 1916 and 1917 and involved the resistance of cotton, *Gossypium* spp., to the leaf blister mite, *Eriophyes gossypii* (Banks), and the black scale, *Saissetia oleae* (Bernard). Field and, later, greenhouse studies of Hessian fly resistance in wheat were begun by the Kansas Agricultural Experiment Station in 1914, and have since continued without interruption. These studies led to the distribution in Kansas of the Hessian fly-resistant wheat selection Kawvale in 1931 and in following years to the distribution of nine wheat varieties derived from hybrids and resistant to the insect.

There are excellent examples of the successful use of resistant crop varieties for control of infestation and damage caused by various insects. Six varieties of wheat, resistant to the wheat stem sawfly, *Cephus cinctus* Norton, are being grown on several million acres in Canada and in Montana, North Dakota, and neighboring states, where wheat sometimes could not previously be produced because of this insect, for which no other economic control measure is available. The availability of cotton varieties resistant to the leafhopper *Empoasca fascialis* (Jack) in South Africa has made the growing of cotton possible where it could not be grown economically before the advent of DDT, and without resistant varieties. Hessian fly-resistant varieties of winter wheat, satisfactory in milling and baking qualities, with high yield, and disease-resistant are available in all the major wheat-growing areas of the United States. More than 20 such fly-resistant wheat varieties are presently recommended by the agricultural experiment stations of the states involved. For the first time a high level of Hessian fly control is available to all wheat-growing farmers at no cost except, perhaps, a small amount for superior seed (Figure 3).

Breeds of animals with demonstrated resistance to arthropod attack have been recognized in recent times only, but reported differences date back much further. An Arabic report of the Crusades indicates that Arabian horses were less bothered by *Hippobosca* ssp. than were European horses. Native tribes of West Africa claim that West African small-humped cattle are more resistant to the attacks of tsetse flies (*Glossina* spp.) and the trypanosomes they transmit than the more recently introduced breeds.

Definite attempts to develop arthropod resistance in domestic animals are difficult to trace. Early in the twentieth century, efforts were made in South Africa to combine the freedom from insects and ticks shown by the Afrikander cattle with the more desirable qualities of European breeds. Results were not gratifying. Somewhat later, European and Asian cattle were crossed to combine the greater resistance to flies and ticks of the Asian cattle with the more desirable conformation of European breeds. These efforts led to the establishment of several breeds that are less adversely affected by biting flies than the

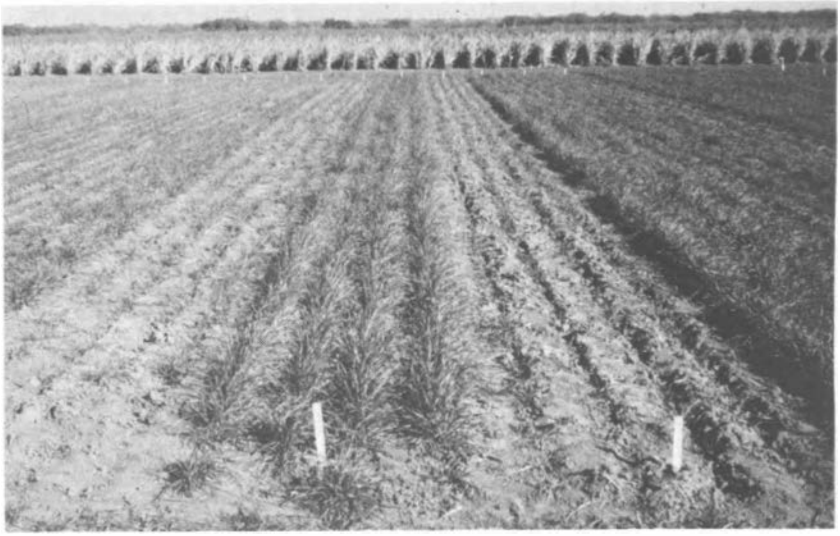

FIGURE 3 Differential fall injury by Hessian fly, *Mayetiola destructor* (Say), to plants of wheat varieties at Hays Branch Kansas Agricultural Experiment Station, October 29, 1962. (Wheat planted September 6, 1962). *Left to right*: Kaw, tolerant; Bison, susceptible; Ottawa, resistant (with stake); Tenmarq, susceptible (with stake); Ponca, resistant; Pawnee, resistant. Tolerant wheats have nearly as many insects at the base as susceptible ones but are less injured. On resistant wheat varieties, few or no flies develop, even though the plants receive just as many eggs as the susceptible or tolerant varieties. (Courtesy of Kansas Agricultural Experiment Station)

common European breeds. Some of the best known lines of purebred Herefords have been selected on a basis of light-colored hair coat, because these strains are less susceptible to the horn fly, *Haematobia irritans* (Linnaeus). Australian sheep ranchers have found that English breeds of sheep are far less susceptible to attack by wool maggots (larvae of several Calliphoridae) than are the Spanish-developed Merino breed. Crosses between the breeds show intermediate resistance.

COMPONENTS OF RESISTANCE

Plants or animals that are inherently less damaged or less infested by a pest than others under comparable environments in the field are called resistant. The term "resistance" is used for beginning studies in the field or in the greenhouse when one does not know what components are involved. Most such cases of resistance are made up of varying degrees of one or more components: nonpreference and preference, antibiosis, and tolerance. These components appear to be generally comparable in plants and animals. Nonpreference and preference refers to a group of host characters and insect responses that lead away from or to the selection and use of a particular host, variety, or breed for oviposition, for food, for shelter, or for combinations of the three. Antibiosis refers to the adverse effects on the insect mortality, size, and life history that result from pests feeding on a resistant host. Tolerance refers to a basis of resistance in which the host shows an ability to grow or reproduce or repair injury while supporting a population approximately equal to that damaging a susceptible host. Each of these components is controlled by one or more genetic factors. Therefore, higher or more stable levels of resistance may often be obtained by combining components of resistance from several sources or by combining genetic factors for each of the three components. Analyses of the component or components of resistance present are needed early in the research, first as a prelude to a separate study of the basis of resistance of each component, and, second, before a separate study of the genetics of each component of resistance is initiated. Only one case is known where two components of resistance are governed by a single genetic factor, the H_3 gene for Hessian fly resistance in wheat. The chemical resistance factor, 6-methoxybenzoxazolinone (RFA), the genetics of which is unknown, is found in corn leaves of inbreds resistant to the European corn borer, *Ostrinia nubilalis* (Hübner). It acts as a feeding deterrent as well as a growth inhibitor; hence, it could be classified both as a nonpreference and an antibiotic component.

Some research workers on insect resistance would confine the term resistance to what is here designated as the component antibiosis. There are at least four reasons for using the term resistance for any combinations of one or more of the components just named. (1) A number of examples of resistance of economic importance include antibiosis as only a minor element, if at all. One example is the resistance to greenbugs, *Schizaphis graminum* (Rondani), in wheat and barley, *Hordeum vulgare* Linnaeus (Figure 4). (2) In studies before the components concerned are analyzed there is no general term except resistance available. (3) The recognition of the three components of resistance emphasizes the importance of finding and, where necessary and possible, genetically combining the components into a single variety to provide the most stable type of resistance. (4) The component of resistance being studied should be defined before studies are attempted on the basis of resistance (Figures 4 and 5). It cannot be emphasized too often that the resistance as first seen in the field generally results from one or more components of resistance, each of which is a complex of interacting factors.

NONPREFERENCE AND PREFERENCE

The nonpreference and preference component of resistance has been discounted perhaps incorrectly in many studies of insect resistance. Increasingly, research

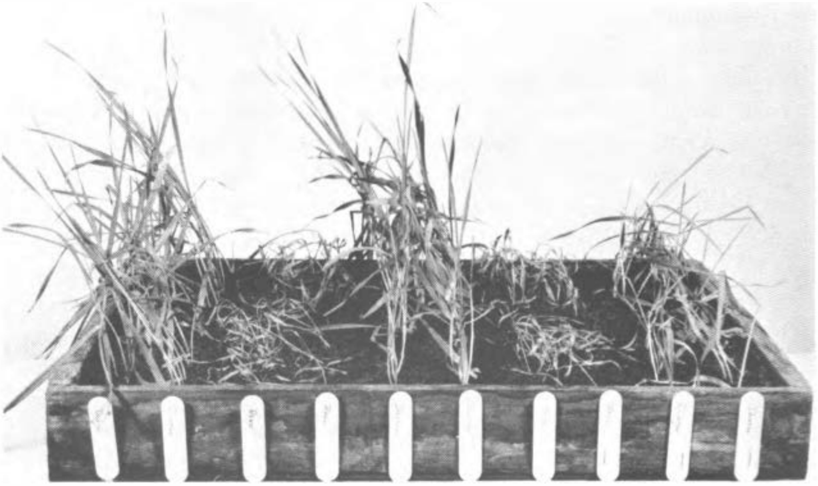

FIGURE 4 Differential damage by greenbug, *Schizaphis graminum* (Rondani), in greenhouse to plants of barley varieties, Dicktoo, resistant (plants healthy), and Reno, susceptible (plants flattened). Reproduction of the aphid is twice as great on the susceptible as on the resistant variety, but the resistant variety carries a high level of tolerance. Compare with Figure 5. (Courtesy Kansas Agricultural Experiment Station)

has demonstrated that inherent responses of insects to inherited constitutents or characteristics of plants are far more stable than previously supposed. Thus, the value of the nonpreferred characteristics can rarely be estimated on the basis of present information.

Insects May Starve Rather Than Feed on Resistant Plants

There are at least two types of nonpreference: first, that which is manifest only in the presence of a preferred host; second, one that can be demonstrated as present in the resistant plant even in the absence of the preferred host. In the latter type, the nonpreference may be so strong that the insect would starve to death, even though no untoward results would follow if it fed on the nonpreferred plant. This was clearly demonstrated by Waldenbauer's studies of the tobacco hornworm, *Manduca sexta* (Johannson), where large intact larvae refused to feed on nonpreferred plants, but larvae with maxillae removed sometimes ate the plants without ill effects. In nature, the original choice or original response to the host after oviposition is made by first-instar larvae or nymphs, which may be more sensitive to the constituents of the host than larger larvae or nymphs. Therefore, it is very difficult to separate extreme nonpreference from antibiosis, or to determine whether the insects starve to death in the presence of adequate food or are poisoned by minute amounts of that food.

Studies on feeding pea aphids, *Acyrthosiphon pisum* (Harris), with a chemically defined diet under various colored lights are examples of extreme nonpreference and apparently are not complicated by other possibilities. In this research, the aphids were given a choice of samples of the same chemically defined diet illuminated by different colors. The insects usually picked the food illuminated with yellow or orange light, and they reproduced abundantly. However, when confined with the same food illuminated only with blue light, they did not feed sufficiently to live or reproduce. On food illuminated with red light, they gained very little and reproduction was poor. When similar artificial food was illuminated with green light, survival was about 50 percent, but weight gained by survivors was normal.

The females of some insects refuse to oviposit on nonpreferred hosts. Others will oviposit on a nonpreferred host near the preferred one but not on a nonpreferred host some distance away. The work on the pink bollworm, *Pectinophora gossypiella* (Saunders), of cotton showed wide differences between ovi-

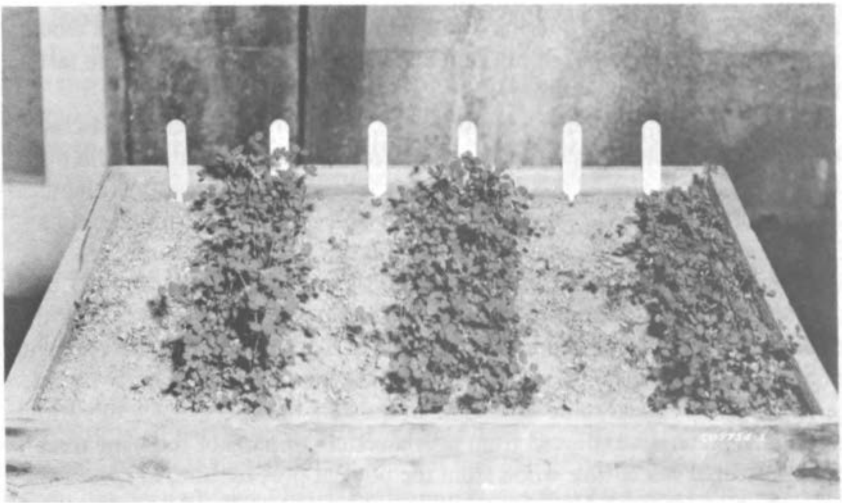

FIGURE 5 Differential damage by spotted alfalfa aphid, *Therioaphis maculata* (Buckton), in greenhouse to alfalfa varieties, Cody, resistant (plants healthy), and Buffalo, susceptible (plants killed). Cody was derived from 22 spotted alfalfa aphid-resistant plants found in Buffalo alfalfa. The resistance of Cody is partially dependent on the tolerance component but is principally due to the fact that the aphid is unable to maintain a population on the variety long enough to kill many plants. Compare with Figure 4. (Courtesy Kansas Agricultural Experiment Station)

position on two species of *Gossypium* both when the two plant species were caged together and when they were caged separately.

The feeding and oviposition patterns in most insects are a complex series of responses to features of the environment and to characteristics of the host. Presumably, the earliest insects found their hosts through random searching, and some still do. Many insects respond to such features of the environment as gravity, light, light–dark margins, and wind movement of a given level. These responses bring them within a range from which they can respond to a specific attribute of the host. Such responses may then take the form of either kineses or taxes. The former provide response to arrestants, the latter to attractants. At first the taxes appear to come from a stimulus for biting or piercing but, later, from a stimulus to continue feeding. As applied to resistance, nonpreference may take the form of one or more breaks in the chain of responses leading to feeding or oviposition. These breaks are the absence of an arrestant or attractant, the presence of a repellent, or an unfavorable balance between arrestant or attractant or both on the one hand, and a repellent on the other.

Most of what is known of the bases of differences in relationships of insects to susceptible and resistant hosts comes from studies of insects on different host species. Less information is available on the bases of interactions between any insect and susceptible or resistant host varieties. Presumably, the same information acquired by the study of differences between host species would apply to differences between resistant and susceptible varieties, but the latter area greatly needs detailed study.

The preference phenomena responded to by insects are extensive, including such physical characters as color, plant surface, internal structure of the plant, and reflection of infrared and other rays. It is generally believed that chemical characteristics are the most important. An insect usually responds to only a few chemicals, and with unbelievable sensitivity when it does. For example, the diamondback moth, *Plutella maculipennis* (Curtis), can taste one 1/1,000 part of the amount of sinigrin that man can taste. A single sensory hair of the black blow fly, *Phormia regina* (Meigen), when touched by a sucrose concentration of 3 one-millionths of a gram per cc of water will cause the blow fly to respond. There appear to be little data on the long-time persistence of various repellents. Materials extracted from resistant trees or parts of resistant trees have protected susceptible wood from the powder-post termite, *Cryptotermes brevis* Walker, for periods of 4 to 11 years.

The value of preference as a resistance mechanism has been questioned by various workers. In a few cases preference appears to be the only component of resistance. It is characteristic of a number of insects with chewing mouthparts where the first-instar larvae on resistant plants take only small nibbles. This is true of the Colorado potato beetle on wild potato, *Solanum demissum* Lindley where the feeding of the insect is limited to small nibbles. The repellent material is apparently demissine, which may also be toxic. Colonies of the insect cannot be maintained on this resistant species. The same small feeding lesions are characteristic of other examples of resistance, including the resistance of some strains of corn to the European corn borer. It is not always clear whether these reduced feedings are the result of extreme nonpreference, or some form of antibiosis, or both.

In Some Animals Pest Feeding Is Not Always Related to Skin Thickness

The component nonpreference and preference is recognized in several species of domestic animals. Horn flies are normally more prevalent on dark-colored areas of an animal than on lighter areas. Significant differences in the preference for dark over light hair coat by horn flies and stable flies have been demonstrated in Holstein, Ayreshire, and Hereford breeds of cattle when the animals are pastured together. However, if light-colored animals are separated from darker animals, they may have large numbers of flies. Lines of Herefords less attractive to horn flies have been developed, but the ease with which these flies can now be controlled by other means has resulted in less emphasis on selecting for nonpreference by horn flies and more emphasis on conformation and efficient food utilization.

Skin thickness has long been suggested as a factor in preference or nonpreference of stable flies, *Stomoxys calcitrans* (Linnaeus), and horn flies occurring on Holstein, Ayreshire, Jersey, or Guernsey cattle. Significant correlations have been demonstrated with the first three breeds but not with the last. No significant differences in the numbers of house flies, *Musca domestica* Linnaeus, feeding on animals of different skin thickness were noted except when biting flies were numerous. Then the house flies fed on drops of blood resulting from the feeding punctures of the biting flies, and the numbers of house flies were correlated with the activity of biting flies and hence indirectly with the skin thickness. The site of skin measurement was important, and measurements on the side of the bovine provided the best estimate of fly numbers, followed by the neck and escutcheon.

Irritability or nervousness of the host has been suggested as a factor in nonpreference of stable flies and horn flies for individuals, and a high degree of correlation has been obtained between the number of flies feeding and the tendency of the animal to frighten the flies away. The heritability of this factor is high but of questionable value in a breeding program.

Nonpreference in ticks for breeds of cattle has been ascribed to several factors, including shorter or thinner hair coat; thicker skin; wrinkled, loose-fitting skin; and differences in the secretions of the sebaceous glands. Some of the tick nonpreference of zebu cattle has been transferred to hybrids with European breeds of cattle. However, the nonpreference of mosquitoes and horse flies for zebu cattle has not been transferred successfully.

ANTIBIOSIS

Abnormal Effects When Insect Feeds on Resistant Plant

The resistance component is called antibiosis when an insect feeds on a resistant plant, and one or more abnormal effects occur: (1) Death of first-instar nymphs or larvae has often resulted, so that the differences between resistant and susceptible plants vary from zero infestation on resistant plants to high infestation on susceptible plants. (2) A lowered reproduction by females reared or feeding on resistant plants is probably the second most common observed effect. (3) Smaller size and lower weight often occur when the effect is not sufficient to result in death of the insect (Figure 6). Sometimes this effect is easily evident; at other times significant differences can only be shown by numbers of measurements. (4) Abnormal length of life frequently occurs either as longer

FIGURE 6 Size of 12-day-old larvae of corn earworm, *Heliothis zea* Boddie, after feeding on corn silks of two different corn hybrids. The larger larva had fed on silk of the corn hybrid Mp317 × 319; the smaller larva had fed on silk of the hybrid F44 × F6. (USDA photograph)

nymphal or larval period, or as shorter adult life compared with insects reared on susceptible hosts. A longer nymphal or larval period exposes the young insect to its enemies for a longer period of time and may lead to fewer generations per year; shorter adult life limits the time available for the female to mate and lay eggs. (5) Smaller food reserves often are accumulated. This affects the ability of the insect to survive if it hibernates and possibly when it aestivates. (6) In a few cases, death has been observed just before the adult stage, thus reducing the population. Hence, death occurs at a time of physiological stress, particularly in an insect with complete metamorphosis. (7) Various behavioral and physiological abnormalities sometimes appear. In the Colorado potato beetle, for example, extra secretions of certain dermal glands, irregular heartbeat, and increased sensitivity to stimulus have been observed. In several insects, regurgitation occurs after feeding on resistant plants.

Experimenters have frequently observed a marked general restlessness when either young or adult insects were caged on resistant plants. This often occurs in species where resistance is considered to be antibiotic but may actually be the result of extreme nonpreference. This restlessness has been commonly observed with aphids caged on resistant plants and with the Colorado potato beetle on resistant potato plants, and it probably occurs with the Hessian fly on resistant wheat plants. In the last case, first-instar larvae normally settle down behind the leaf sheath just above the node, but on resistant plants dead first-instar larvae or small flaxseed (puparia) may be found higher up between the nodes.

Effect of Resistant Plant Variety on Insect Population

In areas where resistant varieties of plants predominate, their effect on the population of the insect resisted is specific, persistent, and cumulative. Since the adverse effects reoccur in each insect generation, most of them tend to reduce the population of the affected pest species. The result may be an elimination of the species in areas where the resistant variety is used. Even a difference of 50% between resistant and susceptible varieties, which is cumulative each generation, would be of high value as a control measure. This actually occurred in Kansas, where the Hessian fly was virtually eliminated for 15 years following the extensive planting of the Hessian fly-resistant Pawnee variety of wheat and other resistant wheats. The Pawnee variety normally carries a level of only about 50% of the infestation compared with susceptible varieties and never occupied 100% of the acreage in any county (Figure 7). The original distribution of Pawnee occurred at the time of high fly population and during favorable weather conditions. Despite this favorable situation, the reduction of fly population occurred. In California the distribution of Hessian fly-resistant Poso 42 and Big Club 43 released in 1942 and 1944, respectively, was followed

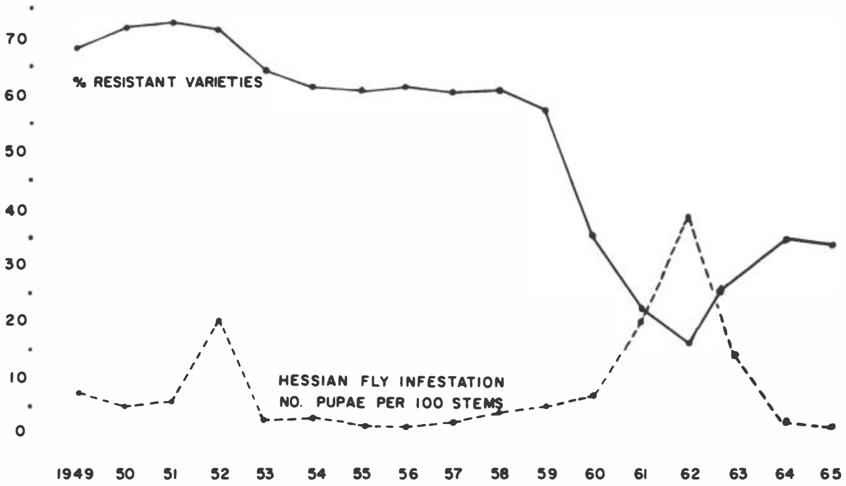

FIGURE 7 Relationship of average percentage of Hessian fly, *Mayetiola destructor* (Say), resistant wheat varieties planted in counties of the eastern half of north central Kansas to Hessian fly infestation, 1949–1965. When the acreage of resistant wheat decreased in 1960, the Hessian fly infestation increased.

by a practical disappearance of the insect from the infested area, and this scarcity persisted from 1942 to near the present time.

The range of differences found in examples of plant resistance believed to be the result of antibiosis is illustrated in Table 1, showing a range from the high-level resistance to the corn leaf aphid and the pea aphid to the 50% or less resistance to the greenbug. The antibiotic resistance shown for the greenbug is accompanied by a considerable level of tolerance and is of high economic value.

Possible Physiological and Biochemical Bases of Antibiosis in Plants

There has been no evidence of a general or single explanation of antibiosis any more than for all three components of resistance as a group (Figures 4 and 5).

A first possible basis of antibiosis is the presence of a toxin in the resistant plant. The term as used here covers a number of possible physiological reactions, which certainly need to be analyzed further as information accumulates. Entomologists and often other people are generally conversant with the fact that insecticides such as nicotine, pyrethrum, and rotenone may be secured from plants. Lists are available of several hundred species of plants containing biochemicals capable of killing insects. Furthermore, varietal differences influence the insecticidal properties of the three insecticides mentioned above. A lethal factor has been reported in silks of corn resistant to larvae of the corn earworm, *Heliothis zea* (Boddie). This has been questioned, but difference in opinion may be related to the presence of the lethal factor in the silks for only a short period of time.

A second possible basis of antibiosis is the presence of a growth or reproduction deterrent or both. For example, gossypol in cotton retards the growth of the bollworm, *Heliothis zea* (Boddie). Resistance Factor A (RFA), identified as 6-methoxybenzoxazolinone, acts as a growth deterrent of the European corn borer; it is possibly the most important factor in leaf resistance to this insect. Resistance Factor A is confined to certain tissues in certain hybrids and also to definite growth periods in the plant.

A third possible basis of antibiosis is the absence of some nutritional materials, such as vitamins, vitaminlike substances, or essential amino acids, in the particular part of the resistant plant eaten by the insect. No evidence for this sort of basis is available except the known sensitivity of insects to deficiency or near-deficiency in some of these substances. In the house fly, for example, absence of certain vitamins in synthetic foods results in death in the first instar, while absence of other vitamins results in death at about the time of pupation.

A fourth possible basis of antibiosis is the deficiency in certain nutritional materials, especially animo acids or specific sterols. In pea aphid resistance in peas, *Pisum sativum* Linnaeus, lower concentrations of amino acids occur in resistant than in susceptible lines. The silks of certain corn lines resistant to the

TABLE 1 Range of Differences in Antibiosis

Insect and Crop[a]	Average Progeny per Female Aphid per Day[b]
Corn leaf aphid, *Rhopalosiphum maidis* (Fitch)	
Sudan 428-1 (R)	0.09
White Martin sorghum (S)	9.85
Pea aphid, *Acyrthosiphon pisum* (Harris)	
Alfalfa plant No. 5 (R)	0.07
Alfalfa plant No. 2 (S)	2.29
Greenbug, *Schizaphis graminum* (Rondani)	
Dicktoo winter barley (R)	1.02
Dickinson spring wheat (R)	1.27
Ponca winter wheat (S)	1.46
Kiowa winter wheat (S)	2.13
Reno winter barley (S)	2.46

[a] (R), resistant; (S) susceptible

[b] Results from various sources and generally at most favorable temperature for reproduction of the insect concerned.

corn earworm also have lower concentrations of amino acids than those of susceptible lines (Figure 6). It has not been shown that this is the principal factor in resistance in either case. Carnitine, lysine, linoleic acid, lecithin, and inositol are other examples of substances reported affecting the biology of particular insects, when deficient in amount. Differences in utilization or digestibility between plant species or even between parts of the same plant are known.

A fifth and related basis could be the imbalance in available nutrients, especially the sugar–protein or sugar–fat ratios. The effect on the growth of larvae of the Angoumois grain moth, *Sitotroga cerealella* (Olivier), resulting from different amylose content of corn grains, may belong in this category, since both high and low amylose-bearing corn lines appear more favorable than certain medium-high lines. Some evidence for bases 3, 4, or 5 comes from studies of food plants of certain grasshoppers, where two plants, which by themselves constitute poor foods, when fed together produce as good growth and survival as a single good food plant.

A sixth basis for antibiosis may involve proliferating tissue or increased secretions of resistant plants, such as that causing the death of eggs or young larvae of the boll weevil, *Anthonomus grandis* Boheman, the melon leaf miner, *Liriomyza pictella* (Thompson), pine resin midges, *Retinidiplosis* spp., and possibly bark beetles, *Dendroctonus* spp.

Several problems are associated with the location of the basis of antibiosis, possibly the most difficult of which is the necessity that work be done with minute first-instar larvae or nymphs. Because the nutritional needs of different insect instars are often materially different, the results with large larvae cannot be substituted for those obtained with first-instar ones. A second difficulty is that the first instars of many insects begin feeding on specific kinds of plant tissue, often meristematic. Therefore, this particular tissue must be analyzed, because general analysis of the entire plant or a large plant part is of little value. A third difficulty lies in the fact that biochemicals concerned are often present in minute quantities and may occur only at certain times in the growth of the plant, times that coincide with periods of attack by the insect, a relationship that probably has arisen through natural selection.

Where a completely artificial food is available for an insect, the study of antibiosis can be advanced by its use. Very few leaf-feeding insects have been reared on a completely refined synthetic food. The addition of yeast, ground leaf tissue, or other substances of unknown composition has usually been necessary for natural maturation and reproduction. The addition to a synthetic food of various biochemicals isolated from resistant or susceptible plant tissues may help solve some of the problems associated with the bases of resistance. No general bases of insect resistance have been found, but extensive investigations may show that certain groups of related biochemicals are involved.

Physical and Antibiosis Differences in Plants Are Rarely Important

Physical and mechanical differences have sometimes been cited as one of the bases of insect resistance in plants. The rice weevil, *Sitophilus oryzae* (Linnaeus), can certainly be excluded by the long husk carried by some corn ears. Common bread wheats with solid straw are resistant to the wheat stem sawfly, although the way in which the solidness affects the insect is not precisely known. However, the relationship between resistance and solid straw has been useful in breeding for sawfly resistance. Hairy cottons in South Africa have been resistant to some species of *Empoasca* spp. leafhoppers, but the same hairy varieties have not been resistant under other conditions to other species of *Empoasca*.

A high correlation coefficient alone is not sufficient proof of the basis of resistance, but a visible character segregating in parallel with resistance is of great usefulness to breeders. Very long tight corn husks may reduce susceptibility to the corn earworm, but to breed for long husks may also mean to breed for short ears, which are sometimes difficult to harvest. Long husks are effective by confining the cannibalistic earworm larvae together so that most are killed, providing more food for the larvae before they reach the ear proper, possibly confining larvae for a longer time on silks deleterious to the larvae, or all three reasons. No full evaluation of these possibilities has been made.

Effect of Antibiosis on Numbers of Pests of Animals

Antibiosis is important in reducing the numbers of parasites on or in domestic animals. Some animals collect many ticks, yet relatively few of the parasites are able to complete feeding on the host. This is particularly apparent in one-host ticks such as the cattle tick, *Boophilus annulatus* (Say), or the winter tick, *Dermacentor albipictus* (Packard). There is little evidence to indicate why these differences occur or the heritability to be expected.

Common cattle grubs, *Hypoderma lineatum* (de Villers), are unable to complete development in one line of Hereford cattle because of the intense irritation that arises in the host when the grub larvae encyst in the back. The fluids that develop in the cyst and the swelling and secondary infection that usually occur cause the death of the grub larva within a week after the cyst is formed. Heritability of this factor is said to be high but of doubtful value in a breeding program because of the severe effect on the host. Antibiosis is also evident at an earlier age during the migration of the larvae through the body to the back. Extensive variations are noted between animals in the number of larvae that appear in their backs when equal numbers of eggs have been deposited on each animal. The factors involved are not yet understood.

Morphological Differences as Basis of Resistance in Animals

During extended periods of warm wet weather, fleeceworm (Calliphoridae larvae) attack of sheep may be extensive. Portions of the body contaminated with urine, particularly the breech of females and the prepuce of males, are most frequent sites of larval attack. Infestation is correlated with heavy fine fleece in these areas, combined with extensive wrinkling of the skin. Merino sheep are usually most severely attacked. They have deep heavy wrinkles around the tail, on the escutcheon, and on the backs of the hind legs. The major predisposing morphological characters are the heavy wrinkling and narrowness of the breech, which permits more soiling of that area with urine and feces.

Breeding to remove the undesirable characters has been successful in several cases. Strains of Merino sheep are under development by breeding for less wrinkled sheep, but progeny-testing of the rams is necessary, because the conformation of the lambs cannot be adequately predicted from that of the parents. The Rambouillet breed of sheep has retained the fine wool of the Merino, but the wrinkles and narrow breech of the Merino have been greatly altered to provide a less attractive morphology to the blow flies of this critical area. Sheep raisers still using Merino sheep may obtain the same results at greater cost by a fold-removal operation (Mules operation), which removes a crescent-shaped strip of skin from above both sides of the tail, down around the vulva for about 2-inches in toward the inside of the leg, to remove excess folds of skin and leave the area relatively free of wool, as it is in the English breeds.

TOLERANCE

The tolerance component of resistance is present when the plant shows an ability to grow and reproduce itself or to repair injury to a marked degree despite supporting a population approximately equal to that damaging or destroying a susceptible host. This component of resistance differs from the other two components in that it concerns a response of the plant, whereas nonpreference and preference, and antibiosis, require characteristics of the plant and an insect response. An understanding of tolerance requires a knowledge of how insects injure plants and how plants repair this injury, and tolerance is more likely to be influenced by adaptation of a variety to climatic conditions. Commonly grown varieties may carry tolerance rather than other components of resistance to an insect that has been present in an area for a long period. Tolerant plants may have more adventitious buds and greater ability to seal off injured parts when attacked by insects with chewing mouthparts (Figure 8). The replacement, regrowth, and repair of tissues are usually dependent on the stage of maturity of the plant at the time of insect attack.

Plant tolerance is possibly present most often in connection with the feeding of insects with sucking mouthparts, such as aphids, leafhoppers, and true bugs. Damage by these insects may result in loss of fluid; loss of food, auxins, and other substances; clogging of conducting tissues by

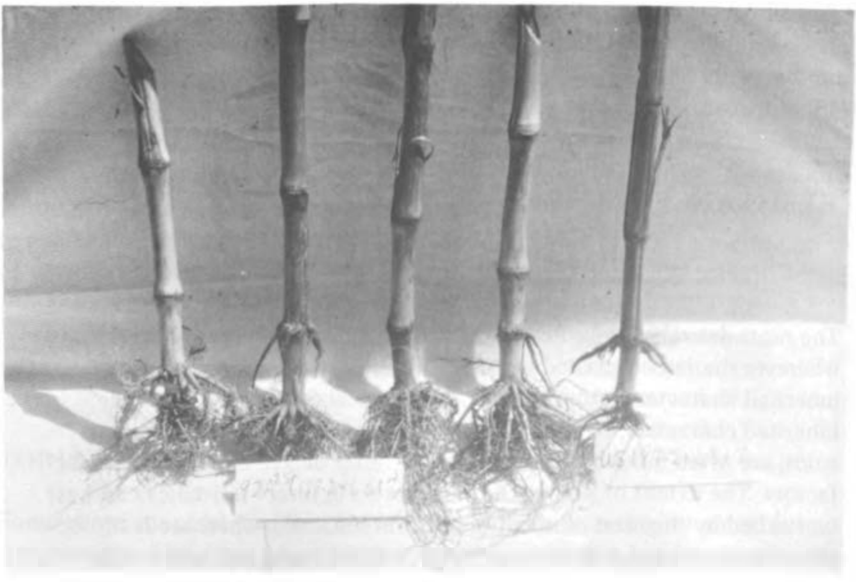

FIGURE 8 Comparative injury by corn rootworms, *Diabrotica* spp., to roots of a susceptible U.S. hybrid 187-2 x L317 (right) and to roots on 4 stalks of a resistant 3-way hybrid involving the susceptible hybrid and a Guatemalan inbred (left). At least part of the resistance is due to the ability of the plant to replace roots faster than they are destroyed. Other components of resistance may also be present. (Courtesy Guatemala–Iowa State Tropical Research Center)

stylet sheath material; and introduction of toxic fluids and enzymes. Together or individually these kinds of damage result in stunting or abnormal growth of the plant.

There has been less research on tolerance than on either of the other two components of resistance. Auxins may play a considerable part in the tolerance component. Studies of the relationship between the two aphids—greenbug and spotted alfalfa aphid, *Therioaphis maculata* (Buckton)–and their resistant and susceptible hosts have indicated that susceptible varieties generally had more free auxins in both quantity and kind than did resistant varieties. This suggests either that the auxins in resistant plants were bound and not available for extraction from the phloem fluid or that the aphids did not reach the phloem or other tissue containing the auxins of the resistant plants.

Tolerance, especially to sucking insects, is greatly influenced by water. The water in the soil of plants being tested with populations of insects can be manipulated to increase or decrease the survival pressures on plants by the insects. Other variables in such research may be the number of insects per plant or the size or maturity of the plants used in the studies.

RESISTANCE FACTORS

MOST DESIRABLE TYPE OF RESISTANCE

The most desirable and most studied type of resistance is one that is valid wherever the insect resisted is a pest; that is, resistance resulting from inherited characters rather than from ecological conditions. However, inherited characters, especially those involving physiological characteristics, are often influenced to a greater or lesser degree by environmental factors. The extent of such modifying factors in insect resistance can best be studied by the establishment of uniform nurseries, where seeds of varieties considered resistant may be assembled, packaged, and sent to various geographic areas to be grown and rated for insect infestation or damage in a uniform manner. Not all the modifying factors mentioned here will be found in any one insect–plant relationship, but the worker should be aware of their possible existence in each case studied. Climate is an important modifying factor. High humidity increases the ease of detection of odors and thus may influence in a positive or negative manner the response of insects to plant odors, thus affecting the nonpreference and preference component of resistance.

SOIL MOISTURE AND NUTRITION

Soil moisture conditions greatly affect tolerance levels in comparisons of susceptible and resistant plants fed on by insects with sucking mouthparts. Under drought conditions, differences between such plants are often more evident.

Edaphic conditions, particularly those concerned with plant nutrition, have often been studied in connection with resistance. The suggestion is sometimes made that the use of fertilizer increases the resistance of plants to insects. The reverse, however, is true in the case of the European corn borer, where frequently the most highly fertilized, most vigorously growing corn carries the heaviest attack. Parallel tests of resistant and susceptible plant varieties under different fertility conditions show that resistance and susceptibility tend to be affected in the same way. Under no conditions of soil fertility has a resistant plant become susceptible or a susceptible one become highly resistant. The review of a number of studies of the effect of soil fertility on the host plant–insect relationship indicates that each species of insect, each host-plant species, and often each type of soil, constitutes a separate problem. Consequently, no general conclusion regarding the effect of a particular nutrient element can be advanced.

Soil nutrition may take one of two relationships to resistance: differences in soil nutrients in small sections of plot tests may be a source of variability in resistance studies, or the soil–plant relationship may provide a mechanism of resistance. Certain plant species and varieties have the ability to extract and utilize various chemicals from the soil with greater efficiency than other species and varieties. If the increased absorption and use of the element contributes to resistance, the ability indicated may be a basis for resistance.

TEMPERATURE

Some genes for resistance to aphids in plants appear to be highly sensitive to temperature. The single genetic factor known in the resistance of wheat to the greenbug is expressed better at temperatures below 24°C than at temperatures of 27°C or above. At higher temperatures it is often difficult to tell resistant from susceptible plants. This temperature–resistance relationship is of minor importance in greenbug control, since resistance is required principally at lower temperatures and indigenous parasites and predators usually control the greenbug at higher temperatures.

The reverse temperature relationship has been true of the resistance of alfalfa, *Medicago sativa* Linnaeus, to the pea aphid and the spotted alfalfa aphid. In both cases a number of clones carrying genetic factors for resistance are more resistant at high than at low temperatures. In the case of resistance to each of these insect species, however, other clones carry a high level of resistance at all temperatures favorable to growth of plants and aphids. In clones that are variable in resistance as related to temperature, the shift from resistance to susceptibility can occur in a relatively few hours. The reverse shift back to resistance takes about the same length of time. Alfalfa clones with genes that are not appreciably affected by temperature, where such can be found, are preferred in practical plant-breeding.

BIOLOGICAL FACTORS INFLUENCING RESISTANCE

Biotypes

In plant-disease resistance studies the development of races of pathogens capable of growing on disease-resistant varieties has been a feature of studies in some diseases. This development of races has not occurred in all plant diseases; however, it is conspicuous in the case of rust resistance in cereals. The growing of an insect-resistant variety may lead to the natural selection of insect biotypes capable of surviving on the resistant varieties. For early recognition of biological strains, the finding of insects of normal size developing on resistant plants, rather than the usual absence of any development or the presence of small individuals, suggests the beginning of the selection of biotypes that will feed on the resistant plants.

The term biotype is used here for groups of insects primarily distinguishable on the basis of interaction with relatively genetically stable varieties or clones of host plants. Such biotypes may or may not be similar to the geographic races of the taxonomist or populations of insects that are distinguishable on other biological grounds. The few cases in which biotypes have developed on resistant varieties are listed in Table 2. The European corn borer is an additional insect for which biotypes related to host plants exist, but no detailed comparative studies of the biotypes on resistant and susceptible corn strains have been made. A possible reason for the relative rarity of biotypes in insect resistance as compared with plant-disease resistance is related to two features of insect resistance. First, there is often the greater complexity in the bases of insect resistance with the presence of two or more components. The second feature is the presence of the host-finding behavior of the insect, which is absent in plant-disease examples.

There apparently are two kinds of insect biotypes in their relation to resistance. In one, exemplified by the pea aphid on peas, the biotype able to feed on resistant plants appears to be simply larger and more vigorous. In the other, such as biotypes of the Hessian fly on wheat and of the aphid *Amphorophora rubi* (Kaltenbach) on raspberry, there appears to be a "lock and key" relationship between a particular insect biotype and a genetic factor for resistance in the plant. Biotype B of the Hessian fly, for example, is able to feed

TABLE 2 Insect Biotypes Involved in Plant Resistance (to 1966).[a]

Insect	Host Plants	Number of Biotypes Known
Hessian fly, *Mayetiola destructor* (Say)	Wheat	4
Aphid, *Amphorophora rubi* (Kaltenbach)	Raspberry	4
Spotted alfalfa aphid, *Therioaphis maculata* (Buckton)	Alfalfa	2
Greenbug, *Schizaphis graminum* (Rondani)	Wheat	2
Corn leaf aphid, *Rhopalosiphum maidis* (Fitch)	Sorghum, corn	4
Pea aphid, *Acyrthosiphon pisum* (Harris)	Peas, alfalfa	3–9

[a] In these examples, geographic populations may be mixtures of biotypes.

on resistant wheat plants carrying the H_3 gene but not on resistant plants carrying the H_5 gene, or genes for resistance from the species hybrid-wheat variety, Marquillo. The lock and key kind of biotype appears to be the most common, and its presence emphasizes the importance of assembling as many genetic factors for resistance as possible in one variety or at least in each insect resistance breeding program.

Plant and Insect Diseases

Another biological factor influencing resistance is the presence or absence of plant diseases on the resistant and susceptible plants. The presence of a disease in a plant naturally changes its metabolism and thus may affect a basis for insect resistance. Insects are frequently vectors of plant-disease organisms and, in at least one example, that of raspberries and the aphid *Amphorophora rubi* (Kaltenbach), varieties resistant to the aphid also are resistant in the field to a mosaic virus carried by the insects; but in the greenhouse the aphid may carry the virus to the aphid-resistant variety.

A peculiar biological feature has been found in one case of an insect disease. When European corn borer larvae feed on certain resistant corns, a protozoan disease organism, which the larvae sometimes carry, may be eliminated, possibly by the action of RFA, so that the few larvae surviving on the resistant plants are healthier and hibernate more successfully than the greater number of larvae surviving on the susceptible plants.

Other Factors

There are many other factors in the environment that may affect the expression of resistance and may be responsible for discrepancies in results secured by investigators under different environmental conditions. That they do occur does not change the fact of the inheritance of resistance that must form the basis of any plant-breeding. Fewer factors affect the permanence of resistance. These mostly concern changes in the genes of either plant or animal, or a small degree of learning on the part of the insect. Such possibilities exist, but experimental evidence or examples of such loss of resistance are rare or nonexistent.

RESISTANCE PROGRAM

RESEARCH PERSONNEL

In the beginning of a new resistance program, the personnel should include at least a competent plant or animal breeder and a well-trained entomologist.

After resistance genes are located and some information is accumulated regarding the genetics of resistance and the biological bases of insect–plant or insect–animal relationships, a biochemist can profitably be added to the team. The cooperative program by members of the team involves not only written agreements but friendly understanding and cooperation in all phases of the work. The breeder should be cognizant of the difficulties and problems in handling the insect concerned; the entomologist should have or develop a genetic point of view in looking at procedures and explanations of developments. Most entomologists are trained to understand the ecological aspects but rarely the genetic possibilities of a problem. As quickly as possible, the entomologist working on insect resistance in plants, for example, should also make himself familiar with breeding procedures and materials in the crop under study, the more important varieties, and particular problems that the plant breeder faces. Moreover, he should understand that unless a new variety, carrying insect resistance, is equal to or better than currently grown varieties in other respects it will not be approved for release; more importantly, it will not be grown by farmers.

It is essential that the entomologist become thoroughly familiar with the insect pest under investigation and also, as far as practicable, its near relatives. The correct identification of all instars of the insect and their type of damage as distinguished from that of other insects is of primary importance. A thorough knowledge of the biology and behavior of the insect is necessary, especially details of the relationship to known varieties of the host plant. This may be secured during or before the initiation of the resistance research. At this stage in these studies a most valuable approach is the field-planting, at different dates, of a series of varieties chosen to represent the maximum range in maturity. Such a plot series will help to separate ecological from genetic effects on insect biology.

INSECT POPULATIONS

An initial problem of the entomologist is maintaining and controlling the insect population so that consecutive tests of a series of crop varieties may be conducted under quite similar levels of infestation as well as other environmental conditions. This continuity can rarely be maintained in the field; it can be maintained more easily in greenhouse or laboratory.

ANIMAL MATERIAL

The development of breeds of animals that show resistance to arthropod attack is not as advanced as the work with plants. Factors involved in this lack of progress include the much greater cost of experimental work, particularly the purchase and maintenance of animals; the longer time required to complete a generation; the usually fewer offspring per generation; and the smaller number of breeds or lines available to the animal breeder. Thousands of varieties of wheat, for example, have been evaluated for insect resistance, but very few animal breeders have access to more than a small fraction of that number of breeds or lines of domestic animals. In spite of the problems involved, research is progressing.

PLANT MATERIAL

Where strains or individual plants (Figure 9) are less injured, sometimes have greater yield, or carry smaller numbers of a pest than nearby strains or individuals of the same species, the presence of resistance may be suspected.

The first plant material to be examined is the locally grown, adapted, or near-adapted varieties, together with those strains being used as sources of disease resistance and other qualities to be incorporated into an improved variety. It is difficult to find an adapted variety already resistant to the insect pest unless it is a newly introduced variety. This did occur in the case of the

FIGURE 9 Alfalfa plant resistant to pea aphid, *Acyrthosiphon pisum* (Harris), among plants badly injured by the insect in farmer's field, Stafford County, Kansas, May 1959. (Courtesy Kansas Agricultural Experiment Station)

spotted alfalfa aphid. When this insect in its early spread reached breeding nurseries, Lahontan, an improved variety resistant to the stem nematode, *Ditylenchus dipsaci* Filipjev, was quickly found also to be resistant to the aphid. There was, however, no relationship between resistance to the nematode and resistance to the aphid, because some of the basic clones used in the makeup of the variety were resistant to the nematode but susceptible to the aphid. The resistance of the other clones to the two organisms was simply fortuitous.

SEARCH FOR GENETIC RESISTANCE

The goals being sought for resistance are genetic characters and not ready-made resistant varieties. If such genetic characters cannot be found in varieties adapted to the region of study, they must be sought in plant varieties of the same crop species or, later, in related species. After studies of local varieties, the first place to look for such genetic factors is in varieties from the original home of the insect or species of the same insect genus. The second area from which to secure plant varieties is the region of maximum variability of the crop under study. The first area depends on the possibility of natural selection for resistance; the second depends on the fact that in areas where visible characters show great diversity, there also may be wide differences in physiological characters that could be the basis of resistance.

An important principle is that the chance of finding genes for resistance is generally in proportion to the number and diversity of plants or animals that can be studied. Plant material to be studied may be secured from other research men working on the same crop; from the United States Department of Agriculture, which maintains germ-plasm nurseries or storage of available varieties of many crop plants; and through the help of the Food and Agriculture Organization of the United Nations. In all cases where sufficient germ plasm has been studied, levels of resistance of economic importance have been discovered. Also, in studies of large numbers of exotic varieties, the varieties more susceptible than those currently grown were more plentiful than resistant varieties. Thus, the introduction of new varieties without known insect resistance may introduce genes for greater susceptibility. As a matter of policy, all new and improved crop varieties, or animal breeds and hybrids, should be routinely tested for reaction to important pests of the crop or animal before being approved or released to farmers by the agricultural experiment station.

Evidence that resistance is genetic comes primarily from a study of progeny of the supposedly resistant host, which are compared, where possible, with standard or susceptible varieties or with the original resistant plant or animal.

To secure such progeny in plant-breeding requires self-pollination of the plant being tested or crosses with a known susceptible parent. The inherited characteristic is the reaction of the plant under comparable environments. If the environment is changed, the reaction may or may not be changed, but if a plant retains its resistance under different environments there is considerable probability that the resistance reaction is inherited. A comparison of the detailed biology or behavior of an insect on possible resistant and susceptible hosts in various places or various environments may suggest inherent stability of the resistance.

In cross-pollinated crops where one or more individual plants resistant to the insect can be found in one or more adapted varieties, such plants can be increased vegetatively or by seed for extensive testing and possible release. This was the procedure by which varieties of alfalfa resistant to the spotted alfalfa aphid were produced. Synthetic varieties produced by interpollination of individual resistant plants may also constitute important sources of selection for resistant factors under various environments.

If the source of resistance is found in a nonadapted variety in a self-pollinated crop, it becomes necessary to cross the resistant plant with another that is adapted to the conditions under study. This may involve choices of sources of resistance and choices of possible susceptible parents. The best parental sources of resistance are those carrying evidence of more than a single component of resistance and, if possible, more than a single gene for resistance. If more than a single source of resistance is available, it may be worthwhile to begin a breeding program in which several sources are used simultaneously, with the possibility of later combining the different genetic factors. The susceptible parent should not only be satisfactory for other agricultural characteristics, but, if possible, it should complement those carried by the resistant line. A single genetic factor, for instance, is easier to manipulate in plant-breeding, but its use may encourage natural selection of insect biotypes that may be able to overcome the resistance of the single gene.

PLANNING EXPERIMENTS

In this early search, the characteristic to look for is the relative absence of insects or insect damage on the individual variety or plant compared with a commonly grown variety. One should not attempt to look for some physical character that the entomologist thinks might be disliked by or be deleterious to the insect. To find and use insect resistance, it is not necessary that the researcher know the basis of resistance any more than it is essential that the plant breeder know the basis of high yield in order to breed for this desirable character. Where funds, personnel, and space are limited, the first tests can be nonreplicated trials. A single test of many new possible sources of resistance is sometimes better than a replicated test of a few possible sources. Varieties or individual plants appearing to be resistant may then be retested on a replicated basis, preferably under various environmental conditions. An important principle is that resistance and not immunity is being sought. Thus, the best infestation level to use is not the highest one that can be secured, but rather the level providing the maximum differences between varieties or plants in the test, or between resistant or susceptible selections, if such are available. If infestations in the tests are too low, varieties of plants or animals escaping infestation may be too plentiful. However, if infestations are too high, valuable sources of resistance may be missed. It is important to plan experiments so that individual plants or animals as well as single plant varieties or animal strains may be studied in a way that will ensure finding resistance due to all the different components.

When a large group of varieties has been assembled, it is worthwhile to consider the possibility of looking for resistance to more than one insect pest, even though primary consideration may have been given to the most important one.

After a possible source of resistance has been found, the next need is to determine, by cage tests if necessary, what component or components of resistance are involved and to be sure that the reaction obtained is genetic and not the result of chance, special ecological circumstances, or the genetic earliness or lateness of the variety under study. Some information on components of resistance may already be available from observation or may be secured from cage tests that compared results where insects were compelled to feed or oviposit on a single variety, plant, or animal with those in which free choice was available.

TESTING PROCEDURES FOR SEGREGATING GENERATIONS

Testing procedures for segregating generations of crosses between resistant and susceptible plants are generally similar to those used in the search for resistance. It is important, wherever possible, to make selection during F_2 and following generations in nurseries where satisfactory insect infestations can be maintained. As in the search for resistance, tests should be designed to reveal the presence of as many components of resistance as possible in a single test or in a series of tests. Test after test and year after year, insect populations should be controlled so that as nearly as possible the same level of infestation is obtained. Here, as in the search for sources of resistance, the tests should be made in the seedling stage of the plant, provided resistance at this stage is correlated with resistance in older plants. The use of seedlings will greatly speed up testing procedures and permit the study of many more plants in the same space. Where insectary and greenhouse tests are made in which pest colonies bred for that purpose (and perhaps consisting of single strains) are used, frequent comparable tests must be made in the field with unselected populations. In some insectary colonies of insects, selections have been made, either consciously or unconsciously, with the result that such populations may not behave the same as the unselected wild populations in respect to hosts.

While the entomological tests in segregating populations are proceeding, parallel tests should be conducted to determine the agronomic or horticultural possibilities of the plant hybrid. When one or more strains approach a variety with the desired qualifications, more detailed replicated tests will be required throughout the area the new variety is expected to occupy. Such tests should be made both with and without the presence of the insect against which resistance is sought and should be designed to give comparisons with currently grown varieties and with improved varieties carrying little or no insect resistance. Information of this kind is needed for submission to committees or others in authority who approve the release of new cultivars. Advantage should be taken of all available agricultural experiment stations in the known range of the insect pest and in the area of probable adaptation of the new plant variety.

RESISTANCE STUDIES

BEST MATERIAL FOR STUDY

Partly in parallel or following the preceding research, a study of the basis of resistance should be made, even though in either plant- or animal-breeding or insect control, information on the basis of resistance is not essential. In plants, such a study should be preceded by thorough biological and behavioral analyses and preferably also by genetic analysis of the insect–plant interaction. Possibly the best material for use in basis-of-resistance studies would be susceptible-and-resistant isogenic lines concerned with a single genetic character for resistance. This would entail the comparison of two selections differing primarily only in the single gene for resistance with its biochemical or biophysical basis.

VALUE OF KNOWLEDGE OF BASES OF RESISTANCE

It has sometimes been suggested that research on resistance should begin with a study of the bases of resistance. Available information on causes in all cases of resistance is not yet adequate for such research at the beginning of a new study; it must wait until sources of resistance are found.

Furthermore, knowledge of one basis of resistance may be of little practical use when seedlings can be screened for resistance by exposure to insects, and many thousands of the plants can be examined in a short time. New and additional sources of resistance with different bases also may be detected when insects rather than physical or chemical tests are used.

A knowledge of the basis of resistance, however, can be of value in a resistance program in two ways: first, to permit screening for resistant plants or animals in the absence of insects; second, with such knowledge it should be possible to combine two noncumulative kinds of resistance in the same variety or breed and be sure both are there. The only other way to do this is through genetic analysis, which might be more time-consuming. Information on the basis of resistance would be of special use in working with resistance in woody plants and in animals, where each generation takes several to many years. In both cases, sources of resistance must be known, or the indirect approach to the study must be used.

The study of the mechanisms of resistance may be useful in other areas of research (see Chapters 12, 13, and 14). In addition to providing basic knowledge of insect behavior and physiology in relation to hosts, it might lead to the discovery of attractants that could be combined with insecticides away from the hosts and used in a search for or destruction of both male and female insects, or at least the females. Repellents, feeding deterrents, or toxins, if found, should be specific and useful, especially if they or related biologically active chemicals can be synthesized. Such supplementary uses may be more valuable than results in connection with resistance.

KINDS OF STUDIES

Studies of the bases of resistance may be either direct or indirect. A direct study involves the comparison of chemical analyses of resistant and susceptible plant or animal strains for differences that can be related to the insect–host reactions of the contrasting resistant and susceptible organisms. An indirect study involves a search for characteristics responsible for attraction of the insect and for characteristic responses normally shown by the insect in the finding of food materials present in susceptible hosts. A comparison with similar attempted isolations from a large number of hosts or from resistant plants or animals may lead to the location of biochemicals concerned with resistance. The indirect approach may provide a knowledge of what compounds to look for in resistant plants.

LIMITATIONS

TIME REQUIRED

The time usually required for the development of a new variety resistant to an insect may be considerable; for a wheat variety it may be 15 to 20 years or more. This objection is, however, more apparent than real. With sufficient funds and personnel there are means of speeding up this time requirement. The comparison ordinarily thought of is with the broad-spectrum synthetic insecticides that have been rather quickly adapted to control of a new insect pest. In resistance, a comparable case is the finding of the alfalfa variety Lahontan, resistant to the spotted alfalfa aphid, which was evident as soon as the insect reached alfalfa-breeding nurseries where this variety was being grown. The resistant variety Lahontan was usable immediately. When resistance can be found in an adapted variety, its use for insect control can be as fast as working out a dosage for an existing insecticide.

Examples of the time required for development of some insect-resistant varieties from the beginning of a search for resistance or location of a specific source of resistance to the release to farmers are: in Hessian fly resistance in wheat–Kawvale, 18 years; Pawnee, 29 years; Ponca, 19 years; in spotted aphid resistance in alfalfa–Cody, 5 years (Figure 10), Moapa, 3 years.

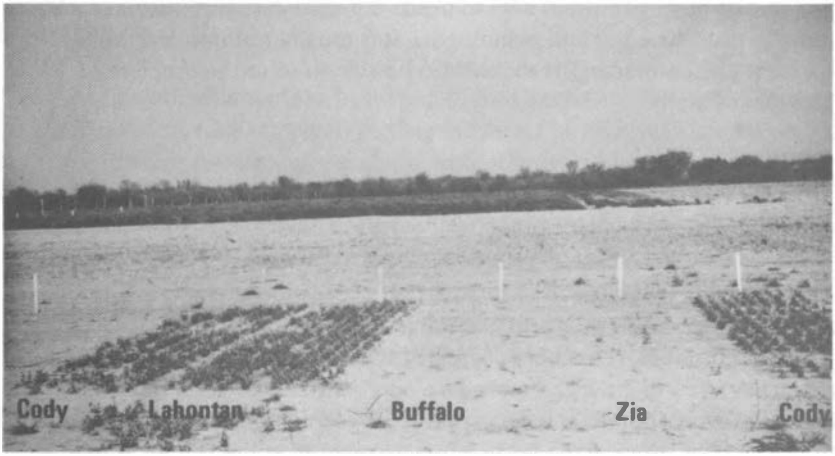

FIGURE 10 Spotted alfalfa aphid, *Therioaphis maculata* (Buckton), injury preceding fall to plants of alfalfa varieties resulted in very low survival of plants of susceptible varieties at the Mound Valley Kansas Agricultural Experiment Station, April 22, 1959. *Left to right*: Cody, resistant; Lahontan, resistant; Buffalo, susceptible; Zia, partially resistant; Cody, resistant. Compare with Cody and Buffalo in Figure 5.

In contrast, development and subsequent use of broad-spectrum synthetic insecticides has been considered relatively brief. Often the time required for synthesis, formulation, and small-scale testing by the patent holder or basic manufacturer, or both, is overlooked by most people. There also are ever-increasing demands for more data on toxicity before an insecticide can get label approval. It would certainly take much longer to obtain label approval now for DDT, heptachlor, dieldrin, and many other insecticides than it did during and immediately after World War II. Techniques for speeding up plant selection and plant-breeding are being constantly improved.

BIOTYPES AS LIMITATIONS

The presence or selection of insect biotypes able to infest resistant varieties can limit the effectiveness of such varieties. The list of known examples is given in Table 2. Such biotypes have not been as much of a problem as the development of races of pathogens in the case of plant resistance to diseases or of insect resistance to insecticides. This may be because of the complex bases of many examples of plant resistance to insects. In contrast, in the natural selection of biotypes resistant to insecticides, the organism is concerned with a single chemical compound, and the basis of plant-disease resistance may also be less complex than that of insect resistance. Although the problem of plant pathogens able to utilize a disease-resistant host is troublesome to plant breeders and pathologists, it is usually not insurmountable. Breeders and entomologists should also be able to solve the problem of biotypes of insects.

INCOMPATIBILITY OF RESISTANCE CHARACTERS WITH OTHER NEEDED CHARACTERS

Another possible limitation of resistant varieties is the incompatibility of factors for resistance with other desirable agricultural or economic characteristics. For instance, it has been suggested that if chinch bugs, *Blissus leucopterus* (Say), fail to grow and reproduce on a resistant sorghum the same might be true of man's domestic animals; yet Atlas sorgo, which is highly resistant to chinch bugs, became the leading forage sorghum in the United States, in part because of its high palatability to livestock. The fact is that insects rarely eat the whole plant and frequently feed in restricted areas not used as food by man or domestic animals, or they feed for only a short time during plant growth. Actually, incompatability has rarely been a problem in insect resistance studies. One example, however, is that of hairiness of leaves of a cotton resistant to leafhoppers, which may present difficulties in ginning because of leaf fragments mixed with the cotton fibers. Hairy cottons have also been reported as more favorable for the development of the cotton aphid, *Aphis gossypii* Glover. It is not certain, however, that the hairiness of leaves of cotton is the only factor in either leafhopper resistance or aphid susceptibility.

REPLACEMENT OF VARIETIES

Another possible limitation is concerned with the replacement of the old susceptible varieties by new resistant varieties; or the replacement of the old resistant varieties, after the insect and its damage are not obvious, by new susceptible varieties, soon accompanied by a return of the pest. If the new resistant variety is also highly superior in agronomic quality, there is usually no problem in its displacing older susceptible varieties, even though farmers may normally be conservative in changes of this kind. After the new resistant variety has decreased the pest population, farmers and agricultural specialists often forget the importance of the insects until the use of a highly susceptible variety again permits an increase of the insect population. The use of secret pedigrees of plant hybrids or varieties by commercial companies aggravates situations of this kind.

OTHER LIMITATIONS

There may be other limitations to the use of insect-resistant varieties. There is little information, for example, regarding the effect of resistant varieties on insect parasites or diseases, especially those that have an obligate relationship to the pest. It is quite possible that with some insect–plant relationships the effect could be adverse instead of favorable. Other problems may occur as resistant varieties come into more general use.

ADVANTAGES AND POTENTIALITIES

EFFECT OF RESISTANCE IS CUMULATIVE AND PERSISTENT

Possibly the most important advantage of the use of insect-resistant plants in insect-pest control has been that the effect of the resistant variety on the pest population is specific, cumulative, and persistent. Near-immunity to the insect is not required. A resistant plant variety that reduces the insect population 50% each generation is sufficient to eliminate in a few generations an insect of economic importance. This quickly cumulative and persistent effect of a resistant variety is in contrast to the sudden and decreasing effect of most insecticides and is possibly unique among insect control measures.

LACK OF DANGERS TO MAN AND ENVIRONMENT

Another important advantage of the use of resistant varieties is that there no problems of toxic residues; of harm to personnel, livestock, and wildlife; of toxicity to honey bees and other useful insects; or of contamination of the environment. These dangers may be present with the use of insecticides.

LOW COST, ADVANTAGEOUS USE, AND POTENTIALITIES

Other advantages include low cost to the farmer, utility in integrated control or pest-management programs, and the fact that a knowledge of attractants or repellents present in natural food plants may lead to the development of synthetic chemicals having these properties (see Chapters 13 and 14).

The potentialities in the use of resistant varieties in the past have been limited primarily by funds and personnel available for research in this important area of insect-pest control. If a fraction of the amount spent on the development and testing of insecticides had been used in the development of insect-resistant varieties, many but not all of our major insect pests of crops might have been controlled or partially controlled by this means. Support for host-plant resistance development has gradually but substantially increased in recent years, as state and federal administrators have reduced emphasis on chemical-control investigations and have stressed noninsecticidal means, including host-plant resistance.

VALUE OF LOW LEVELS OF INSECT RESISTANCE IN PLANTS

The value of low levels of insect resistance in plants (Figure 11) has not received the attention it deserves. A low-level resistant variety with considerable tolerance, combined with the use of parasites or predators, may provide a satisfactory type of integrated control without insecticides. The host insect may furnish a steady supply of food for a parasite or predator, thus preventing its extinction, while at the same time the pest inflicts little or no damage to the host plant. There are instances where an insect cannot be controlled adequately on susceptible varieties even with repeated treatments by insecticides, whereas control can be achieved on resistant varieties with few treatments, if

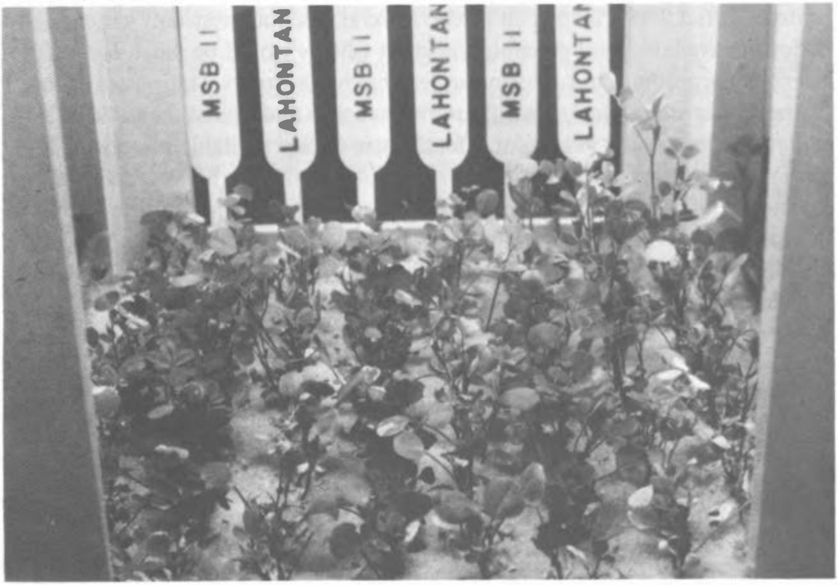

FIGURE 11 Varietal difference in alfalfa seedlings infested for 3 weeks with one potato leafhopper, *Empoasca fabae* (Harris), per two plants at 21°C. MSB-11 is resistant and Lahontan is susceptible to leafhoppers in the field. Here, the leaves of Lahontan seedlings are yellowish to reddish in color, and growth has been suppressed. The leaves of MSB-11 are deep green, and growth has been normal. (From Kansas Agricultural Experiment Station)

any are needed. The corn earworm on sweet corn in the southern United States is an example of the former situation; the spotted alfalfa aphid on alfalfa illustrates the latter.

SITUATIONS WHERE INSECT-RESISTANT PLANT VARIETIES ARE MOST USEFUL

The use of resistant varieties is most valuable in crops of low value per acre, especially where yields fluctuate greatly because of weather and other intermittent hazards, or under situations where insecticidal control is unknown, unavailable, or too costly. Resistant crop varieties should be of special use in the developing countries where acreages worked by individuals are small and farmers are unfamiliar with the use of insecticides. A form of insurance can be provided by resistant varieties where the insect resisted shows wide fluctuations in populations, with outbreaks several years apart. The greenbug in the central United States is such an insect. Several greenbug-resistant varieties of barley are available, and greenbug-resistant wheats would be most useful. The insect can reproduce and destroy susceptible barley and wheat plants at low temperatures when the ordinarily useful parasites and predators are inactive and at temperatures too low for effective use of any available insecticide. Yet greenbug resistance is relatively higher at low than at high temperatures.

The use of an insect-resistant variety of one crop may reduce the population of the same insect on another crop as well. In areas where corn earworm-resistant corn varieties are used in the southern United States, the damage by the same insect on cotton, where it is known as the bollworm, is reported to be reduced also, since there is a smaller total population. Where both alfalfa and peas are grown and subject to infestation by the pea aphid, a pea aphid-resistant alfalfa should reduce the problem with this insect on garden peas. In these respects the usefulness of host-plant resistance to insects is often unique among control measures.

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CHAPTER 7

Control by Parasites, Predators, and Competitors

One of the oldest and most successful methods of controlling insect and related pests is by using their natural enemies—parasites, predators, and disease organisms—to attack and destroy them. Disease organisms and their use are considered in Chapter 8. Parasites and predators have received much attention, and they are discussed at length in this chapter, together with insect competitor displacements. The use of competitors to suppress pest populations is a recent idea.

The deliberate use of natural enemies for pest control is widely known as biological control, or biocontrol. Man has known for many centuries that insects attacking crops were in turn attacked by many kinds of natural enemies that, at times and in certain places, exerted a high degree of control over the pests. It was not until about 100 years ago, however, that deliberate attempts were initiated to use these enemies in control activities, either by introducing new ones to the environment of a pest or by increasing the effectiveness of species already present.

The first demonstrations of effective biological control resulted from a recognition of the fact that in various parts of the world many agricultural pests are aliens—immigrants that have spread from other areas and become established in new homes, either fortuitously or by the movement of agricultural and forest products through man's commercial activities. The first noteworthy demonstration of biological control occurred in California in 1888. Entomologists about that time discovered that many pests that became established in new environments often did so unaccompanied by the full spectrum of natural enemies that attacked and often controlled their populations in the countries of origin. The idea was conceived of bringing these enemies from the native homes of the pests and releasing them in the new environments to attack the immigrant pests. For many years, this movement of natural enemies dominated biological control activities, and even today it receives a major share of the effort devoted to the biocontrol method.

Although the work in California toward the end of the nineteenth century was not, strictly speaking, the first involving the movement of natural enemies, it is generally agreed that it established the method as a valid and useful device for pest control. In 1887 the developing citrus industry in California was seriously threatened by the cottony-cushion scale, *Icerya purchasi* Maskell, and many growers were forced to abandon their plantations. No sprays or other chemical treatments known at that time would control the scale. C. V. Riley, a prominent entomologist, suggested that the original home of the scale was Australia or New Zealand and that natural enemies of the scale should be introduced to California from these countries. The idea found immediate favor, and in 1888 Albert Koebele, an entomologist, was sent to Australia for this purpose. He soon found a small lady beetle known as vedalia, *Rodolia cardinalis* (Mulsant), attacking the scale in the Adelaide area, and in November 1888 the first shipment of the beetle reached California. The beetles in this and later shipments were liberated immediately on scale-infested trees and they soon completely cleaned the trees of the scale. Within a year, a startling and highly effective degree of control had been obtained throughout the citrus-growing area of the state at a total cost of less than $2,000. To this day, the vedalia continues to provide completely satisfactory control of the cottony-cushion scale in California, and the savings it has brought to the citrus industry of the state have been incalculable.

Since 1888, projects in biological control have been conducted all over the world, and many of them have been successful. Effective programs of biological control have been established in many areas, from Japan to West Africa and from Canada to Australia. More than 110 different pests in more than 60 countries throughout the world have been controlled by the use of parasites and predators. Canada and California have been especially active in this field and have recorded 15 and 18 successes, respectively. Success is directly related to the research effort expended on biological control, and the number of pests effectively controlled may increase dramatically as more and more countries turn from excessive reliance on pesticides to the promise offered by the biocontrol method.

Considerable emphasis has been given to biological control at several centers in the United States and Canada, and the United States Department of Agriculture has played an important role in its development. In addition, several international organizations have been established specifically to conduct research on biological control and to facilitate the movement of beneficial species between countries. The largest of these is the Commonwealth Institute of Biological Control, established in 1927 to work on biological control in the British Commonwealth. The Institute has major laboratories in Switzerland, Trinidad, India, and Pakistan and maintains small field stations in a number of other countries. It is equipped and prepared to conduct biocontrol research and exploration for natural enemies throughout much of the world at the request of any country willing to provide financial support for its activities.

Another international organization for biological control is the Organisation Internationale de Lutte Biologique, formed by a group of Western European nations to foster biological control and to stimulate and facilitate the movement of natural enemies across their borders. Many other countries have devoted considerable effort to biological control; especially noteworthy are Australia, Russia, Japan, and Israel.

ADVANTAGES AND KINDS

Biological control, as defined here, has a number of distinct advantages not offered by most other approaches to pest control now available. Three advantages are permanence, safety, and economy.

Biological control is relatively permanent once it is established. The natural enemies on which it depends are self-perpetuating, barring natural catastrophes or the unwise interference of man, and they continually adjust to changes in the population size of the pests they attack. There are a few examples of insect hosts having developed resistance to their parasites, which interfered with successful biological control. It may be that any host–parasite or predator–prey interaction involves a continuing adaptive race between the antagonists, with the fed-upon species moving constantly toward greater protection from attack and the attacker compensating by becoming more effective. In most cases for which information is available this race seems continuously unresolved, and effective biological control has a high degree of permanence.

Biological controls have no side effects such as toxicity or environmental pollution, and they are not hazardous to use. In the current concern over the quality of the environment in which we live and over the possible consequences of continued long-term exposure to nontoxic levels of pesticides, the advantages of biological control are being weighed more heavily when decisions are to be made on the best strategies for pest control. However, biological controls should not be thought of merely as useful and safe alternatives to chemical controls; they should be thought of as offering distinct advantages and having unique features in situations where they are applicable.

There are three main kinds of traditional biological control, each of which is discussed in detail in this chapter. These are:

1. Introduction of exotic species of parasites and predators. This entails the search for natural enemies in foreign countries, their introduction to areas where the pest is causing damage, their rearing, and their release. The principle underlying this approach has already been mentioned: many pests were accidentally introduced to new areas without their normal complement of natural enemies. These enemies may be found in the native home of the pest, or in the home of a close relative, and reassociated with the pest. Most of the successes achieved with biological control have involved introduction, and much contemporary research and activity centers on this approach. Two other approaches, however, have increasingly been added to this preoccupation, and this complementary trend in interest will undoubtedly continue and perhaps even accelerate.

2. Conservation of parasites and predators. This emphasizes the importance of making full use of natural enemies that attack a given pest in a particular location, regardless of whether they are introduced or native. The best opportunity for accomplishing optimal use of parasites and predators is by changing their environment in ways that will increase their effectiveness and thus reduce survival of the pest. In its simplest form, this has involved the adjustment of pesticide programs to prevent harm to the beneficial species. In a more complex form it may entail the alteration of single or multiple environmental factors that restrict the effectiveness of beneficial species by reducing or regulating their abundance at points below the optimal. Such manipulations can only stem from very broadly based and intensive research at the systems level in pest-management programs.

3. Augmentation of parasites and predators. This approach, sometimes called inundation, involves the mass-rearing and periodic release of large numbers of a natural enemy of proven value. Releases are made over small areas, with the objective of temporarily raising the abundance of natural enemies to a high level at times when the pest is most vulnerable to them.

ECOLOGICAL BACKGROUND

In the 1950's, biological control was a clear-cut entity, readily separable from other forms of insect-pest control, and easily defined. It was the suppression of the numbers of pests by exploiting the biological attributes of certain organisms, principally parasites, predators, or competitors that are antagonistic to the welfare of pest species. Such organisms were usually called "natural enemies," not a particularly appropriate name, because enmity was not involved in the relationship and many of the organisms were unnaturally introduced or propagated in the environment. At that time, two other broad classes of control were recognized: cultural and chemical control, each readily distinguished from biological control.

However, a host of new ideas for controlling pests has since been introduced, few of which clearly fall into any of the older categories. Instead, they tend to fall between them and could logically be included in two or more of them. Thus, there is a tendency for the old boundaries to merge and blur, and clear-cut distinctions have become lost. This tendency has been encouraged by a trend to use various controls in combination, so that one type supplements or reinforces another type to produce maximal suppression of the pest, with minimal deleterious side effects.

The old categories, however, still serve a useful purpose. The concepts behind them, while changing, are still valid in principle. The names applied to them designate activities whose outlines still have enough clarity to make them useful; thus, biological control is still a useful term to designate activities in which parasites, predators, and competitors are used to suppress pest populations.

The basis of biological control is intimately involved with the theories of larithmics (Greek *laos,* population, + *arithmos,* numbers). In an effort to understand the basis of their art, biological control workers have contributed extensively to larithmics, and it is now difficult to know which ideas were derived from which source.

Basic to the theory of biological control is the concept of community homeostasis: all living things constitute components of self-regulating communities and as such are subjected to naturally occurring regulative processes that tend to maintain a degree of numerical balance between all elements of the community. According to this concept, the biological activities of each organism impinge on, and interact with, the activities of some of the other organisms that share the same general area. Thus, a web of action and interaction is generated that both amplifies and restricts the activities of each organism, the sum of all activities forming a coherent, integrated unit—the community. The community is thus a fairly abstract idea; its boundaries can rarely be delimited, and its characteristics can seldom be clearly defined. Nevertheless, that the community is an entity is clearly shown by the facts that competitive and antagonistic organisms do live and persist on the same site and that each depends on at least one other kind of organism for the essentials of life and for many subtle benefits. This is discussed in Chapter 3.

Predators (including parasites) have long been recognized as important elements in the dynamics of arthropod communities. It was recognition of the high degree of interdependence between predators and their prey that gave rise to the idea of density dependence. Observations of natural populations revealed that as a prey population increased in numbers an increasing proportion of them were killed by predators, and as it declined in numbers a decreasing proportion were killed by predators. The mechanism was thought to work as follows:

An increasing prey population provides a surplus of easily found food for predators, and the surplus permits the predator population to expand. As the predator population expands, an increasing proportion of prey is killed by predators before the prey reach maturity, the process progressively decreasing the rate at which the prey population can reproduce. Eventually, such a large proportion of prey is killed that the survivors are too few to produce as many offspring as were produced by the previous generation, and the prey population declines, usually precipitously. Fewer prey provide less food for the predators, and prey become more difficult for predators to find. Thus, the predator population, faced with a shortage of food, declines even more precipitously. Relieved of excessive predation, the prey population is again free to expand until once more checked by a revived predator population. This mechanism constitutes a less than perfect, but nevertheless effective, regulating system that maintains populations of both prey and predators within certain fairly narrow limits of abundance and scarcity.

A system dominated by forces such as these agrees with a cybernetic system in the process of "hunting." The force initiating change in the system is the inherent capacity of the organism to increase in numbers by reproduction; the counter-force generated within the system is predation of individuals before they achieve reproductive maturity. The system "hunts" because the degree of predation can neither be exactly proportional to the change in the prey population nor exactly synchronous with the change. This can be demonstrated simply.

As long as the proportion of reproductive females in a prey population surviving each generation exceeds the inverse of the mean number of offspring each can produce, the population will increase; if the proportion is less, the population will decrease. Thus, if each female can produce X offspring, the number of offspring in generation $n + 1$ will exceed the number in generation n when more than $1/X$ of the individuals born into generation n survive to reproduce; if less than $1/X$ survive, the number of offspring in $n + 1$ will be less than in n.

Consider a prey population in which less than $1/X$ of the individuals have escaped predation in generation n. At the conclusion of that generation there must be a predator population capable of destroying at least $(X - 1)/X$ of the prey individuals. If the predator population was able to overcome the prey population it must have a reproductive potential approximately equal to or greater than X. At the end of generation n, both predator and prey populations reproduce. The new prey generation will be $X(<1/X) = <1$ times the previous generation, while the new predator generation will be at least $X[(X - 1)/X]$, or $X - 1$ times the previous generation. At the start of generation $n + 1$, the number of prey is less than at the start of generation n, but the number of predators is severalfold that of generation *n*. Thus, there are enough predators in generation $n + 1$ to kill all the remaining prey; the only prey that escape are a few not found by any predator. Most of the predators do not find enough food in generation $n + 1$ and die before maturity. Therefore, both populations decline precipitously to very low levels.

Because at least one prey is needed to support each predator, and because at low population densities a decreasing proportion of the prey is found by predators, the number of surviving predators must be substantially less than the number of surviving prey. Thus, the prey population is relieved of excessive predation and starts to increase again. This, in turn, provides more food for predators, and the predator population can also start to rise. But the efficiency with which predators can find prey remains fairly low until prey density increases to certain levels, after which predators gain efficiency and, in the presence of a surplus of easily found food, multiply rapidly at the expense of the prey population until they finally overwhelm the prey again.

Therefore, predation, the corrective force of this system, is never proportional to the changes induced by the reproductive capacity of the prey population, nor is it ever fully synchronized with these changes. In the early stages of a cycle, when the prey population starts to increase, the response by the predator population is weak and delayed. In the final stages the response is overpowering and is maintained beyond the appropriate period. The system is therefore inherently unstable and cannot be called upon to produce community stability. It could, however, and probably does, constitute a principal device by which the observed fluctuations of natural populations are generated and sustained and by which such fluctuations are contained within certain limits.

This model, of course, is a gross oversimplification of the processes occurring in natural communities. If this were the only mechanism influencing populations, fluctuations would follow periodic cycles of abundance and scarcity. Such regular cycles are no more a feature of natural populations than is stability of numbers. A vast number of factors other than abundance of and searching by predators affect the survival of prey, and a similar number of factors other than number of prey influence the survival of predators.

Weather, for instance, can be considered a population-determining device; it includes a great number of everchanging elements that strongly influence populations of all kinds of organisms. It can affect populations either directly, by influencing the physiology of the organisms themselves, or indirectly, by affecting the quality and quantity of foods and shelters. By either route, weather may cause populations to expand or collapse. However, neither favorable nor unfavorable weather is generated or modified by any feature of the populations acted upon; weather acts impartially on all populations, regardless of their abundance or stage of growth. Such elements cannot contribute to regulation; rather, they are agents that modify the workings of the homeostatic system, sometimes amplifying it, sometimes short-circuiting it, always introducing unpredictable variations into its workings.

A simple, two-element relationship postulated by the predator–prey model is not likely to exist in any natural community. Most prey populations are attacked by several kinds of predators, and each kind attacks in a different manner, with a different intensity, and at a different time, and each responds differently to changes in prey numbers as well as to variations in weather. Moreover, only a few kinds of predators are completely dependent on a single kind of prey and therefore may not respond directly to changes in abundance of any one kind of prey as required by the predator–prey model. The quantity, quality, and distribution of foods, on which the survival of all prey populations is dependent, are governed by weather, soil composition, and the number of other organisms feeding on the same commodity. Predators of predators can influence the success of the latter. These are but a few of the multitude of factors that can affect the numbers of both predators and prey quite independently of any direct interaction between them.

The regulation of natural communities is obviously a much more complex phenomenon than is indicated by our simple model. Nevertheless, most population ecologists consider that some variation or elaboration of this theme forms the basis of community stability. Two forms of population-determining forces are at work: nonreactive forces, usually of extra-community origins, which act independently of the affected populations; and reactive forces, usually generated by living agents within the community, which are evoked by changes in the affected population itself, and which tend to counter such changes, although imperfectly. Nonreactive forces are mainly meteorological, geological, and, to some extent, man-made forces—man-made because man, although an organic entity himself, must be considered an element apart from organic communities when he demands special concessions from community mechanisms. Reactive forces are mainly the so-called “natural enemies,” that is, parasitic, predacious, and competitive organisms. Combined, the nonreactive and reactive forces provide the motive and opportunity for evolutionary adaptation. Either of the forces may determine the level of any given population at any given time; only the reactive forces, however, can maintain a population between finite levels of abundance, i.e., only they have homeostatic properties.

APPLICABILITY OF BIOCONTROL

When genuine pest situations are found to exist, the most appropriate strategies for controlling them must be determined. Biocontrols are not suitable to every pest situation; they may be suitable only as a part of a broader strategy that includes other devices. Before biocontrol procedures are initiated, they should be thoroughly justified on the basis of biological and ecological information. Definite and specific flaws in the regulative structure of the community should be recognized, and a reasonable possibility of alleviating or correcting these flaws by practical biological manipulations should be established.

Some features of pest communities that may influence the feasibility of biocontrols are: gaps existing in the natural-enemy complex, which might be filled by introducing new natural enemies; native natural enemies that possess attributes of good control agents but are inhibited by some lack or maladjustment of the community; ineffective native natural enemies that might be replaced by more effective foreign ones; the degree of pest suppression needed to achieve control (economic threshold); the suitability, costs, and degree of protection achievable by other kinds of controls; and the probability of undesirable side effects that may accompany certain controls, such as pollution, toxic residues, damage to other organisms, resistant strains of pests; and preservation of esthetic values. The recognition and resolution of these matters require a careful analysis of the pest community. Until a substantial body of community information is available, no rational strategy can be evolved.

COMMUNITY STUDIES

The amount of information necessary to launch a biocontrol program varies with the urgency and complexity of the problem. Some situations require immediate action, and sometimes experienced workers can take such action on an intuitive basis. But a carefully planned and executed investigation of the pest situation is usually essential for the development of a rational program.

Essential information may consist of only a chronological life history of the pest and its major natural enemies, plus a gross description of the physical environment. However, a long and complex analysis of community relationships may be needed to determine the factors regulating the pest, to estimate the stages of the pest most vulnerable to attack, and to determine the kinds of agents most likely to succeed in suppressing the pest.

Biocontrol programs usually begin with a minimal investigation. If actions taken on that basis fail, the investigation becomes more and more detailed—leading to new and presumably more sophisticated actions. The kind of information required for a minimal investigation is much the same as that required for the initial stages of an in-depth investigation. In starting a project, therefore, it is wise to conduct the first steps so that the information gathered is usable for an in-depth investigation if such should become necessary.

Virtually every pest situation is unique; therefore, the research methods applied to investigate each situation must be unique and must be devised by the researcher as he develops his program. In developing a program, the researcher should have specific questions in mind and should gather and assemble data in such a way that answers to these questions are revealed. Unfortunately, this advice is not always easy to follow, especially at the outset of an investigation, because a certain amount of information must be available before the right questions can be asked.

The first steps of an investigation should be designed to reveal a broad spectrum of general information from which explicit questions are generated. A good starting point for such a program is the life-table system as evolved by Morris and his co-workers. It is doubtful that their system can be directly applied to any pest other than the spruce budworm, *Choristoneura fumiferana* (Clemens), in spruce-fir forests, but the system is amenable to modification to meet a wide variety of situations. The virtues of the system are that it provides direction for the purposeful gathering of data and that it presents those data in an informative manner. The system asks its own questions, assigns objectives to the investigation, and delineates the population parameters that must be estimated to achieve these objectives. It eliminates much of the aimless data-gathering that is often a feature of this type of investigation. The disadvantages are that the system requires several independent population censuses of each generation of the pest, that several (about 5) sequential generations must be censused, and that these censuses should be conducted simultaneously in several different kinds of sites. Thus, a project based on this system cannot be considered a short-term one. However, a considerable amount of information is revealed by a life table of a single generation on a single site, perhaps enough to suggest specific questions answerable by short-term experiments, or perhaps even enough to suggest control measures.

The characteristics of a good research program for a biocontrol project are that it provides broad-spectrum information quickly, that it is capable of development into a long-term program that will reveal even more information, and that it clearly defines the essential data that must be gathered. The life-table system possesses all these characteristics to a high degree. The system is also simple, easy to understand, and readily analyzable.

TYPES OF PEST SITUATIONS

There are two basic types of pest situations, each requiring a somewhat different outlook by the researcher. These are designated A and B. Type A occurs commonly in forest environments: in this case the long-term mean of the population, or the "steady density," is well below the level that causes significant economic damage, but occasionally the population increases rapidly, and very high populations cause severe damage for a period of one to several generations. Such periods are called "outbreaks," or "epizootics." They eventually decline, usually precipitously, and the population resumes its usual low level. Type B is more common in agricultural environments: here the mean population level remains consistently above the economic threshold, and although population fluctuations occur, they often are small in amplitude. Differences between the two types are partly brought about by inherent differences in the species of pests involved in each, partly by differences in the intensity of cultural practices carried on in the two environments, and partly by differences in the kind of damage inflicted and in the amount of damage that can be tolerated in the two environments.

In Type A situations, the mean level of pest abundance is satisfactory if the population would stay at that level. Short of extermination, it is probably impossible to lower the population mean enough to prevent peaks of outbreaks from exceeding the economic threshold. The problem, therefore, is to stabilize population fluctuations. Thus, we are concerned with the factors that cause change in the numbers of pests. Mortality factors that are stable, that take a fairly constant toll of the pest, are of little concern except as they reduce the effective reproductive potential of the pest population. However, they usually constitute the major portion of the total mortality affecting the population, killing perhaps well over 90% of each generation, even during periods of population increase. However, mortality factors that vary in their effect from generation to generation are of great concern, even though these factors may contribute only a minute portion of the total mortality. This apparent anomaly can be easily illustrated. Suppose a pest female can produce 100 eggs. If the sex ratio is 1:1, only 2 of the 100 eggs can survive if the population is to remain constant. Thus, if mortality is less than 98% in any one generation, the population will increase; if it is more than 98% the population will decrease. Now suppose that 95% of each generation is killed by constant mortality factors, and another 4% may be killed by a number of variable factors. When all variable factors are effective, 99% of the generation is killed, and the subsequent generation is halved; when some of these factors are ineffective, and perhaps kill only 1% of the generation, the subsequent generation doubles. Since there may be a number of these variable factors, each may contribute less than 1% of the total mortality. Yet these factors determine the fate of the population. Morris has discussed this type of situation thoroughly.

Type B situations may stem from two causes: the pest numbers may be consistently high, and therefore in excess of the economic threshold; or the economic threshold may be very low, in which case even quite scarce organisms may exceed it most of the time. In neither case are fluctuations the primary cause of concern; it is the mean population level that is significant, and our interest centers on the agents that determine the mean level. These may be agents that are fairly stable, and that, in total, take a fairly constant proportion of the pest population. Our objective here is to lower the mean population below the economic threshold and to maintain it at that level by arranging a complex of constant mortality agents that on the average destroy a portion of each generation equal to, or exceeding, the reproductive potential of the species. Only when this condition is approximated do population fluctuations, and their causes, become significant, and then only if the peaks of fluctuations exceed the economic threshold.

Many pests clearly fall into one or another of these classes: The spruce budworm is a typical Type A pest, and the codling moth, *Carpocapsa pomonella* (Linnaeus), is typical of Type B. Many other pests, however, fall somewhere between the two; they fluctuate widely in abundance, with a mean abundance close to the economic threshold. When their numbers exceed the mean, they exceed the economic threshold; when they drop below the mean, they are below the economic threshold. In such cases, whether emphasis should be centered on the mean level or on fluctuations of the population is a matter of judgment.

LIFE HISTORIES, ECOLOGY, AND BIONOMICS OF ENTOMOPHAGOUS SPECIES

The life histories, ecology, and bionomics of entomophagous species are included in one heading because it is difficult to recognize where one ends and another begins. They are all investigated to provide information regarding the probable effectiveness of the organisms as regulators of the target pest and to estimate the probability of successful establishment of the organism in a new region.

Entomophagous organisms vary widely in their food-getting habits; they range from typical parasites to typical predators, but between these extremes a virtual continuum of forms can be found. Typical parasites differ from typical predators in that the former usually require only one organism (the host) to complete larval development, whereas the latter usually require several organisms (prey) to achieve maturity; parasites are usually attached to, or contained within, the host throughout their larval stage, but predator larvae are usually free-living; host-finding by parasites is usually a function of the female parent, while predator larvae or adults of both sexes usually must find and capture their own prey; parasites usually do not kill their host until long after their attack, but predators usually kill their prey immediately on encountering them. Almost any combination of these characteristics may be found in a single organism, and many organisms do not clearly fall into either of the categories. However, these differences are real for a large body of entomophagous organisms, and they profoundly affect the form of interaction between parasites and hosts and between predators and prey.

Because a typical parasite, once established in or on a host, usually has its total food supply secured, it has an excellent chance to survive to maturity regardless of the number of other hosts that may be parasitized. The parasite larva escapes the problem of finding additional food from a diminishing supply. Thus (ignoring such complicating matters as multiparasitism and superparasitism, and the occurrence of some extraneous event such as predation or other death of a parasitized host), each host attacked by an adult parasite is fated to die before reproductive maturity, yielding at least one new adult parasite. If more than one parasite is produced from each host, a situation could develop in which a highly parasitized host population yields more parasites than hosts, triggering a population fluctuation.

Each predator, however, must search for and find its own prey and must continue to find additional prey throughout its entire life. Each captured prey is instantly removed from the prey population; the amount of food available to each predator is reduced, and the probability of each one getting enough food is lessened. When prey are depleted to a certain level, some predators die of food deficiency. Further depletion of the prey population is accompanied by a simultaneous depletion of predators. Thus, the corrective force of this system (predation) tends to be in phase with and proportional to changes in the prey population. This mechanism dampens tendencies for change in the system and promotes stable populations.

Parasites

The mode of life adopted by parasites has greatly limited their freedom of action; they have become highly adapted to certain niches and have virtually cut themselves off from all other niches. In particular, the larval stages of parasites have become intimately connected to, and dependent on, a narrow range of hosts both for a living environment and for food. A given species of parasites attacks only hosts possessing certain specific characteristics found in only a few species (oligophagy), or, in extreme cases, in only a single species (monophagy). Very few parasite species have a wide range of hosts (polyphagy). But such is the diversity of parasites that few arthropods are free of them.

The two organisms (host and parasite) must be in an identical microhabitat when both are in the appropriate stages of development, respectively, to give and receive the parasite egg. This process involves two phases: a close chronological coincidence of life histories of the two species and an innate behavior that leads the parasite to the vicinity of the host.

Synchronization of host and parasite development is supported to a large extent by the almost complete dependence of the larval parasite on the physiological processes of the host, which is important in ensuring coincidence of the remaining stages. It also eliminates many phytophagous species as potential hosts of a given parasite. Because time of emergence of the adult parasite is influenced by the development of its host, the adult parasite is more likely to be synchronized with the same host species than it is with other species that have no influence on the chronology of its development.

From the viewpoint of bionomics, the adult stage of parasites is of major importance, for it is this stage that determines the number of new parasitizations and the hosts that are to receive them; it is the female adults that seek out and select hosts and lay or withhold eggs. From the time it emerges from the pupa, the adult parasite must carry out a series of steps which ultimately lead to the distribution of viable eggs in, on, or near suitable hosts. The number of steps and the manner in which they are taken vary widely between parasite species: the manner of oogenesis and spermatogenesis; the time of, conditions for, and manner of mating; the manner and time of egg fertilization and maturation; the searching behavior of the female; the manner of oviposition; and the selection of hosts for larval development all profoundly influence the success of parasite reproduction and the consequent fate of the host population.

The time required for each of these processes, and whether they can be completed at all, is often dependent on environmental variables extrinsic to the parasite or host. Factors such as temperature, moisture, light intensity, and day length are strongly influential; also, many adult parasites require certain foods to carry out these processes. Parasites moved to new ecosystems are not likely to achieve a high degree of success unless suitable environmental conditions prevail and food and other requisites are available.

Parasite–host synchronism is of particular concern when the transfer of a parasite species to a new environment is contemplated. The parasite must be placed in the new environment at precisely the right developmental stage and at the right time, so that gravid females are ready to oviposit on, in, or near hosts when the latter are vulnerable to parasitization. The period of host vulnerability may be brief.

Before the act of parasitization can take place, the adult parasite must find suitable hosts. The mechanics of parasite-searching probably include two principal phases: a behavior mechanism that brings the parasite into the general vicinity of the host and a sensory mechanism that permits perception and recognition of suitable hosts. The biological bases of both phases are undoubtedly complex and probably vary widely among the diverse kinds of arthropod parasites. It is important to note that a host that inhabits one sort of environment is not likely to be found by a parasite that is attracted to another sort of environment. Thus, it is improbable that a host that inhabits deciduous trees will be parasitized by a parasite that is attracted only to coniferous trees, even though the former may constitute a perfectly suitable host in all other respects. Similarly, even though a parasite and a phytophagous species coinhabit a certain environment, successful parasitizations are unlikely if the parasite cannot detect or recognize the phytophagous species as a potential host. These factors are important in the determination of parasite specificity.

The ability to find hosts varies widely among parasites. Some species seem efficient at finding hosts only when they are abundant; when the host density is low, these parasites experience difficulty in finding enough hosts to sustain a viable population. Such species often possess a high reproductive potential and are able to expand their numbers rapidly when there is an abundance of hosts; thus, they are able to overcome and suppress pest populations of outbreak proportions. Other parasite species have a very highly developed searching capacity and find hosts even at low densities. Many of these species, however, have only a moderate reproductive capacity; therefore, their ability to overtake an expanding host population is poor. Although such parasites probably will not be fully effective in suppressing a high population of pests, they are able to hold a low pest population at a low level of abundance for extended periods.

These characteristics of parasites are not necessarily mutually exclusive. Both characteristics, i.e., high searching ability and high fecundity, are important to biocontrol programs. Which characteristic is more important in any given case depends on the prevailing situation and the role the parasite is expected to fill.

Predators

Although predation is a common and highly significant biological function, remarkably little is known of its mechanics or its role in population processes. Classical predation theories have little basis in demonstrable biological fact. A large array of complex variables conditions every predator–prey interaction, and it is probable that no two situations are conditioned by identical sets of factors. Thus, each predator–prey situation is undoubtedly unique. But certain basic elements condition every situation, and all situations are therefore basically similar.

In all predator–prey situations, the number of prey destroyed by predators is a product of two universal elements: the number of predators present and the number of prey killed per predator. Each of these elements generates a different sort of population response: that concerning the numbers of predators is called the numerical response; that concerning the number of prey consumed per predator is called the functional response. Each type of response is conditioned by the number of prey present; i.e., predators may respond to changes in prey density by altering their own numbers (numerical response) or by altering the number of prey each predator captures (functional response), or both. Numerical responses are a product of the quantity of food available to predators, and they operate through reproduction, immigration, emigration, and mortality processes. Functional responses are generated by behavioral and physiological processes of the predator and by the essential mechanics of the act of predation itself, i.e., by searching, discovery, handling time, digestion, hunger, competition between predators, and prey defenses. The degree to which predators respond either numerically or functionally to prey abundance strongly influences their regulative function in the community.

Although most predators have not specialized to the same degree as parasites, oligophagy is not uncommon. But polyphagy is more common. The distinction between the two classes is not sharp; the range of prey available to oligophagous predators is narrow, whereas polyphagous predators can exploit a wide range of species. The terms “narrow” and “wide” are relative and defy sharp distinction. The difference between the two, however, is more than one of convenience; it reflects real differences in the probable bionomic effects of each of the classes.

Oligophagous predators, because of their dependence on a narrow range of food organisms, may exhibit a numerical response to the abundance of certain prey. Polyphagous predators are less likely to respond numerically to changes of abundance of any prey species. If a given prey is in short supply, one or more other species can be substituted for it, and the predator population survives unscathed; conversely, an abundance of a given kind of prey is not likely to improve the chances of predator survival unless the predator population was previously limited by an absolute shortage of prey. With a wide range of prey available to polyphagous predators, the latter condition is probably rare.

In certain communities that lack faunal diversity, some inherently polyphagous predators may be forced into oligophagy by the absence of suitable alternative prey species. In such situations, they may respond numerically to changes in the abundance of the only available prey in the same manner as do oligophagous species. Such situations are exceptional, however, and do not reflect the general characteristics of polyphagous predators.

The usual role of polyphagous predators is assumed to be nonregulative. Because of their relative freedom from limitations imposed by restricted food supply, polyphagous predators are thought to maintain rather constant numbers. If there are no preferences for certain prey, the number of individuals taken from each of the potential prey species will be a function of the number of encounters between individual predators and individuals of each of the prey species present. This is obviously a product of the number of both predators and prey present, modified by the amount of activity conducted by each. The numbers of predators are considered to be practically constant, and the activity of each species is a fairly constant characteristic of the species. As a result, changes in the numbers of individuals of any one prey species captured by polyphagous predators are mainly conditioned by, and proportional to, the numbers of individuals of that species present. From generation to generation of the prey species, therefore, polyphagous predators take about the same proportion of individuals from any given prey population.

Some polyphagous predators undoubtedly respond functionally to changes in the abundance of certain prey species; some facet of behavior, physiology, or psychology may enable each predator to capture more individuals of a specific prey population when that population is abundant than the same predators capture when the prey population is low. Such a functional response to the density of certain prey has been shown for a large number of predators. If a polyphagous predator does exhibit a functional response to the density of a particular prey, it will generate a regulative feedback system similar to that generated by oligophagous predators.

Synchronization of life processes is not such a critical element in predator–prey relationships as it is in interactions between parasites and their hosts, because predators are usually less intimately involved with the physiology of their prey than parasites are with their hosts. But, as with parasites and hosts, predators and prey must come together in a common habitat before predation can take place, and the prey must be detected and recognized as a food. Thus, searching is as important to predators as to parasites and probably contains the same essential elements. Moreover, predators must be able to overpower their potential prey, thus introducing the elements of relative sizes of predator and prey, aggressiveness, armament, and tactics of the predator and defenses of the prey. Many predators overcome their prey by brute force; in such cases, the predator must be larger, stronger, or better armed than the prey. But other predators are able to overcome prey many times their own size by means of artifacts such as trip lines, snares, or pitfalls. Prey defenses may consist of cryptic or warning colors, obnoxious scents or tastes, or protective hairs, spines, or armor. Only in a very few cases is the effectiveness of these devices known. The usual anthropocentric interpretations are highly questionable: Who knows what is obnoxious to an insect?

Genetic Factors

In the selection of entomophagous organisms for colonization, the question arises of their fitness to survive and prosper in their new home. This is a two-sided problem: first, there is the degree to which the organism is preadapted to the colonial environment; second, there is the degree of postcolonization adaptation that can be expected from an organism.

It is significant that about 80% of all completely successful cases of biocontrol were accomplished by a single species of natural enemy, and in most cases control was achieved promptly, usually within three generations of the introduction. Obviously, the successful organisms were well preadapted to both the target host and the new environment. Precolonization adaptation, therefore, seems a highly desirable feature of a species selected for biocontrol.

The degree to which preadaptation exists in an organism is undoubtedly a reflection of similarities between the endemic and colonial environments. Thus, an obvious generality is that immigrant species should be sought in areas climatically and geographically similar to the proposed new home. But, however similar two areas may be, they are not likely to be identical, and if introductions of entomophages were confined to thoroughly preadapted species, biocontrol activities would be severely restricted. However, for most potentially valuable biocontrol agents some degree of postcolonization adaptation is probably essential, and in some cases the degree of necessary adaptation may be considerable.

Entomophages in general, and parasites in particular, tend to have fairly rigid behavior patterns and are tolerant of only a narrow range of conditions. This is a result of the highly specialized life they have adopted, which has permitted large numbers of species of similar habits and behavior to coexist in close proximity to each other with minimal competition. In the process, each species has limited itself to a restricted habitat and has largely lost the ability to encroach on any other habitat. This feature of entomophages severely limits their ability to adapt to new situations. To promote colonization of new territories, therefore, the colony founder should be selected, if possible, with the objective of promoting new gene combinations and consequent rapid changes of population characteristics.

Population genetics and the effects of environment on the genetic structure of populations are complex subjects that are imperfectly understood. Thus, it is unwise to make unqualified statements regarding them, and any statements made here would be grossly oversimplified and misleading. But ideas arising from these subjects deserve much more attention from biocontrol workers and should lead to serious reconsideration of some of the established biocontrol doctrines.

For example, the usual approach to this problem has been to obtain organisms from as wide a range of sources as possible, on the assumption that adaptation will be facilitated by including in the colony the full range of genetic variation existing in the gene pool of the entire species population. However, there are good reasons to conclude that this practice may actually inhibit rather than enhance the potentiality of the colony to adapt. Strongly heterozygous populations are normally in a state of stable genetic balance, and innovations arising in such populations tend to be rigorously suppressed. If genetic innovation is desired (and only through innovation can adaptation develop), it is more likely to arise and survive in small populations originating either from the margin of a heterozygous population or from a population recently subjected to catastrophic reduction of heterozygosity. Such populations are inherently unstable genetically and generate a multitude of new genetic combinations in what Mayr has called a "genetic revolution."

Thus, efforts to establish colonial populations by introducing large numbers of individuals from widespread source populations, in addition to being a very costly procedure, may be largely self-defeating. A series of much smaller colonies, each originating from a single, preferably isolated, population pocket, may offer greater opportunities for successful postcolonization adaptation.

PROCEDURES AND TECHNIQUES

INTRODUCTION OF EXOTIC SPECIES

The introduction of exotic species is often considered the main, if not the only, role of biological control, and it is emphasized in many treatises on the subject. Most examples of successful biocontrol reported in literature have resulted from its use. The strategy has proved outstandingly successful in a substantial number of cases. In many more cases, however, intensive and sustained efforts to apply bicontrol in this way failed utterly or, at best, produced only partial control, often of somewhat doubtful authenticity. Many of the failures were caused by attempts to apply the strategy to inappropriate situations; a need or purpose was not first established, and no clear-cut objectives were defined.

There are only two kinds of conditions in which the introduction of exotic natural enemies is appropriate: situations in which there are unoccupied niches in the life system of the pest, which could be filled by an introduced species; and situations in which a certain niche is occupied by an organism that is inherently inefficient as a regulator and that might be displaced by a more efficient exotic regulator. Unless there is a reasonable probability that one of these conditions exists, and unless exotic organisms appropriate to these conditions can be found, introductions should not be contemplated.

Although these are the only conditions under which introductions can be justified, their occurrence in pest situations is widespread. The first condition is usually fulfilled in the common case where the pest itself is an introduced species. Many phytophagous insects find their way to new lands; some discover a very favorable physical environment and ample supplies of food there. They are slow to adjust to the organic communities of their new homes, however, and, more important, indigenous communities are slow to adapt to the immigrants. Thus the immigrant species do not enter into community interactions in the new ecosystem, and they are able to expand their numbers free of community restraints. The only effective limitation to their abundance is the supply of food, which they exploit at an ever-increasing rate. Since the exploited foods are often plants of economic significance, such insects become major pests.

These pest situations are often caused by a lack of entomophagous agents that are adapted to prey upon the immigrants in the new community; thus, there are unoccupied niches in the life system of the pest. Filling these niches with suitable species introduced from the endemic range of the pest is a remedy for this situation.

Gaps may even occur in the life systems of indigenous pests, especially pests in highly modified communities where the native control agents may have been virtually eliminated. The possibility of filling these gaps with introduced entomophages should not be overlooked.

The possibility of displacing an inefficient native entomophage with a more efficient foreign regulator exists in many pest situations. Displacement of one organism by another comes about through competition between ecological homologues in a common environment. One of the competitors possesses some advantage, however slight, over the other and gradually gains access to the total supply of some niche requisite, thus denying this requisite to the other competitor. The second competitor, progressively deprived of a requisite, gradually declines, yielding place to the first.

Ecological homologues are usually defined as genetically distinct organisms occupying identical ecological niches. The niche is considered to be the role played by an animal based on its precise food, spatial, and habitudinal requirements in a particular habitat. What an animal does and what it needs as requisites for survival and reproduction in a given habitat determine its ecological niche. It seems highly unlikely that genetically distinct organisms can occupy identical niches, and it does not seem essential to the concept of competitive displacement that they do so; the niches need only be similar, with at least one but preferably with a number of common essential elements. Two organisms occupying different but overlapping niches in a single ecosystem will come into competition for common requisites, and the more successful will deprive the less successful of a requisite, thus displacing it. The more similar the niches, and the more elements they have in common, the more positive and rapid is the displacement; the less similar, the more dubious is the displacement.

Competitive displacement should be a powerful biocontrol tool, but which homologue will survive when two are brought together in a common habitat is virtually unpredictable, and it is not certain what makes one homologue a better pest regulator than another. Presumably, a high ability to find prey is advantageous in this respect, but this is very difficult to measure. Reproductive rate also should be an important consideration, but the actual rate at which the population can increase from one generation to the next is what is important, and this is contingent on many environmental variables, including community interaction. However, the effective reproductive rate of an organism placed in a new environment is largely unknown.

For practical purposes, it is assumed that a regulating agent that displaces a homologous agent does so by some form of closer utilization of the prey population, thus reducing the prey to a lower level than formerly prevailed. If this assumption is valid, it is unnecessary to evaluate the potentialities of an exotic homologue; all that is needed is to introduce the candidate species into the pest community. If the new species displaces its established homologue, it will do a superior job of pest suppression; if it does not displace the established homologue it will be eliminated, with no harm done. This generalization, although convenient, is somewhat superficial, and should be recognized as a facile working hypothesis rather than an established ecological principle.

An extended period of intensive taxonomical and ecological research should precede any responsibly conducted introduction of a foreign organism. Not only should it be shown that no harm is likely to follow the introduction of an exotic species, but also that the particular organism selected for introduction possesses particular attributes that are likely to be beneficial to the particular community in which it is to be established.

All good biological research depends on sound taxonomy. First, the identity of the involved organism must be known; this is the key to the store of accumulated knowledge about the organism. Without this key, knowledge can neither be extracted from the store nor added to it. Moreover, poor taxonomy may lead to the wrong store of information, with disastrous results to an investigation. Many biocontrol programs have foundered on poor taxonomy. Extended and costly actions have sometimes been taken as the result of an incorrect identification, and the possible solution of the pest problem was unnecessarily delayed.

There is an even more significant reason for good taxonomy. The best taxonomy demands that the essential uniqueness of each kind of organism be understood and that the elements relating the organism to and differentiating it from other similar forms be recognized. The acquisition of such information is basic to biological manipulation.

Lack of adequate taxonomy can constitute a very significant obstacle to biocontrol programs. Many of the species encountered are new to science or little known. Proper diagnoses and descriptions of such entities are major undertakings, often requiring generic or family revisions. Persons qualified to undertake such projects are rare and are usually fully occupied. For some groups of organisms, no qualified taxonomists exist. Biocontrol workers must often fall back on their own resources in these matters, and some have become recognized authorities in the taxonomy of certain groups.

FOREIGN EXPLORATION

The search for entomophagous species in foreign areas is based on the fact that plants and animals transplanted to new lands sometimes flourish and become pests because they have escaped the natural enemies that suppress them in their native habitats. Introduction of these natural enemies into the invaded habitats may result in lowered abundance of the pests.

There are no great mysteries in the organization and execution of a foreign exploration program. If certain logical steps are followed, there is an optimum chance for success. As indicated previously, foreign exploration is largely conducted for parasites and predators of pests of exotic origin. There are exceptions to this rule, and programs have been undertaken or advocated for introduction of exotic natural enemies against indigenous pest species. But the results have not been highly rewarding, for the obvious reason that indigenous pests are usually already attacked by adapted natural enemies.

In California, for example, important imported natural enemies have been established on about half of the most serious scale insect, mealybug, and aphid pests—all exotic species. In fact, in every case in which significant natural enemies have been introduced into California since 1888, the pest involved has been an immigrant species. It is difficult to imagine a similar degree of success against such native pests as the corn earworms, *Heliothis zea* (Boddie); a lygus bug, *Lygus hesperus* Knight; a leafhopper, *Erythroneura elegantula* Osborn; the banded-wing whitefly, *Trialeurodes abutilonea* (Haldeman); a leaf miner, *Liriomyza pictella* (Thomson); the cabbage looper, *Trichoplusia ni* (Hübner); and the western spotted cucumber beetle, *Diabrotica undecimpunctata undecimpunctata* Mannerheim.

The usual initial step in natural-enemy introduction is to confirm that the pest of concern is of foreign origin. This is usually a simple matter, normally resolved through perusal of the literature, examination of museum material, and, most importantly, consultation with taxonomic experts in the group of insects to which the pest belongs.

However, some pests are of such wide distribution or have existed in invaded environments for so long that it is difficult to determine whether or not they are native. The beet leafhopper, *Circulifer tenellus* (Baker), is a case in point, as are such cosmopolitan aphid species as the cotton aphid, *Aphis gossypii* Glover; the green peach aphid, *Myzus persicae* (Sulzer); and the pea aphid, *Acyrthosiphon pisum* (Harris). An important but not infallible criterion for determining the status of such pests is whether or not specific or highly adapted natural enemies occur on them. If none occurs and the pest exists in chronically epidemic abundance, there is reason to suspect that it is of foreign origin. For example, the pea aphid and the walnut aphid, *Chromaphis juglandicola* (Kaltenbach), both exotic species, existed as major pests in California for over half a century free of significant parasitization. This was a glaring signal to those attempting control of the aphids to consider searching for parasites overseas. But little or no thought was given to parasite introductions, perhaps because the two aphids had occurred for so long in the California environment that economic entomologists literally accepted them as components of the native fauna. However, in the late 1950's, when parasites were obtained from overseas, they readily became established and quickly became of primary importance as enemies of their respective hosts.

Once it has been determined that a pest is of exotic origin, the next step is to pinpoint its native home and determine as precisely as possible its distribution in the area of indigeneity. Examination of taxonomic papers or other important literature concerning the pest or related species, study of museum material, and consultation with taxonomists or workers on the pest's biology, ecology, or control will usually provide information on its foreign origin and area of distribution. However, these measures sometimes fall short of this goal, and additional sleuthing is necessary. In certain cases, the host-plant affinities of the pest can be used to localize the insect's native home, particularly where the host range is highly restricted.

At times, the areas of origin of certain pests have been indicated by information available at the ports of entry through which the insects apparently invaded new lands. Jet air transport has altered this situation, however, since insects can now be rapidly carried hundreds or even thousands of miles inland without passing through seaport areas. There has been speculation that the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), reached New Mexico from the Old World in this manner.

Whatever the situation, it is of utmost importance that multiple criteria be invoked in any attempt to determine the area of indigeneity of a pest. If this had not been done with the spotted alfalfa aphid, the search for its parasites might have been centered in India, the area from which Buckton described his *Therioaphis maculata*. Instead, systematists and other entomologists were consulted on the aphid's taxonomic status, distribution, and the occurrence of parasites on it. These inquiries revealed the pest to be of very wide distribution, with its taxonomic status in a state of confusion, and its parasites virtually unknown. Therefore, the search for parasites was conducted over a wide area, including Western Europe, the Middle East, and India. After intensive search, three parasite species were found in Europe and the Middle East, but none was found in India. Thus, if taxonomic criteria alone had been used and the search for parasites restricted to India, the program would have failed.

By the time the foreign explorer embarks on his odyssey, he usually knows where he is going and has a considerable knowledge of the pest he is seeking, its appearance, habitats, habits, hosts, behavior, biology, phenology, distribution, and recorded parasites. He also will have made arrangements with his colleagues for receipt and handling of the material to be shipped in, and he will have worked out details for his operations in the country to be visited. His job then is to find the pest, obtain its natural enemies, if such exist, and tranship them in viable condition and adequate numbers to the receiving laboratory.

In searching for the pest and its enemies, a variety of collecting techniques may be used, those adopted depending on the nature of the host species and the natural enemies themselves. Such techniques are known to the experienced or well-trained entomologist.

In seeking out habitats of the pest, there is no special need to penetrate into the most remote and inaccessible places to find effective natural enemies. Excellent collecting can be done in parks, botanical gardens, street-side and dooryard plantings, weedy places, and croplands, as well as in areas of undisturbed native vegetation. It is sometimes advisable to collect from agricultural plantings, on the premise that parasites and predators occurring in such environments may have adaptations enabling them to flourish in crop plantings in the invaded area.

The foreign collector must keep in mind the possible scarcity of the pest species he is seeking in its area of indigeneity. This is to be expected where the species is attacked by effective natural enemies. The pest will sometimes have a colonial distribution, occurring in abundance only in scattered, highly localized foci. These foci often represent populations that for some reason have temporarily escaped the repressive influence of their natural enemies. Such infestations can provide excellent collecting, particularly where the factors inhibiting natural-enemy activity can be eliminated and a sequence of collections can be taken. A situation of this type may be of special benefit when large numbers of the pest are needed for the rearing of its parasites.

The duration of a foreign exploration program and the area covered by it will vary with the nature of the problem, the agency conducting the search, the distribution of the pest, and the complex of the pest's natural enemies. Some programs have been conducted from permanent or semipermanent stations and have extended over vast areas. Other programs have been of very limited scope and duration, being restricted to the collection of one or two species over a short period of time in a single area.

The search for a pest's natural enemies, when undertaken for the first time, should normally be programmed to extend over at least one full season of the pest's (or enemy's) activity and should cover as much as possible of its distributional range. This permits sampling for enemies of the pest's various growth stages as well as those with different phenologies and peculiar ecological requirements. For instance, the alfalfa weevil, *Hypera postica* (Gyllenhal), an essentially univoltine species of very wide distribution, is affected by a variety of parasite species that attack all its growth stages. These parasites vary in phenology and in distribution. In any given area, optimum collection of egg parasites, for example, occurs weeks before that of pupal parasites. Furthermore, certain parasites that flourish in the cooler, more humid areas of the weevil's distribution are extremely rare or even nonexistent in the hotter drier areas. These factors have been taken into account in the alfalfa weevil-parasite introduction program in the United States, which has extended over many years and a vast area.

It is possible that a pest or any given parasite or predator, or both, may exist in several ecological or biological forms. The possibility of sibling species existing in both the pest and natural-enemy categories must also be taken into consideration.

From this brief account, it should be quite clear why the foreign collecting activity should have dimension in both time and space, especially where a program is being undertaken for the first time. Obviously, there are many situations where all factors cannot be taken into account during one season, and this is why certain programs have been protracted over many years.

SHIPMENT OF PARASITES AND PREDATORS

Criteria for the shipment of living insects are in many respects similar to those for any perishable commodity. Frequently, the shipments represent the end results of an extensive program of investigation, collecting, and rearing. If the insects perish in transit, it is difficult or impossible to replace them, at least until the next season. Therefore, the care and expense of shipping should reflect the fragility of the packaged insects as well as the ease with which they can be replaced. It is always advantageous to convey shipments as quickly as practical and to maintain them within a reasonable range of temperature while in transit.

Modern air transport has greatly reduced the time for shipment; international services are available between all the major cities of the world, and national services reach other centers in most countries. The frequency of flights is being greatly accelerated, and flight times are being shortened. Air cargo can be used for overseas shipments; it is expensive, but there are no practical restrictions on size and weight, living material is assured priority shipping space in heated and pressurized compartments, and the shipment can often be scheduled to arrive on a specific flight. Airmail is much cheaper but often takes slightly longer in transit, cannot be assured of special care, and is more likely to be subjected to adverse conditions. Air express can be used for intercontinental shipping.

Personal contacts with airline and postal officials are important in avoiding needless delays and hazards. When air cargo is used, scheduling should minimize the number and length of transfers both between and within airline companies. Shipments should be delivered to the carrier in sufficient time for documenting but should be retained under suitable physical conditions as long as possible. Consignees should arrange for quick personal delivery rather than depend on ordinary services. If insects are sent over short distances by air express, overnight flights ensure their arrival and delivery early the following day.

Basically, the shipping container must be rigid enough to withstand the rigors of its voyage and soundly constructed to prevent the escape of any insects that are active or might become active en route. Usually, the same collector or agency ships a variety of insect species and stages, and there is an advantage in using a universal container that can be easily adapted to a specific need. Many shipping containers used for air cargo transfers are of wooden construction, allow some air circulation, have provision for maintaining humidity, and can be modified to allow adult emergence in transit, as well as feeding facilities, if necessary. Insects sent by airmail are often placed in cardboard mailing tubes or plastic containers provided with aeration. Such packaging is suitable if the conditions encountered are not extreme.

Since most shipments are made during warm weather, and modern aircraft holds are maintained above freezing, high temperatures represent the greatest hazard to the survival of insects. This can be lessened by the use of vacuum flasks or foam-plastic insulation that will maintain desirable temperatures during air transfer. Vacuum flasks provide better insulating properties per unit thickness and are less bulky; but they are more fragile, are manufactured for a different purpose, cannot be manipulated as can plastic materials for more-suitable construction, and cannot be readily adapted to refrigeration with reusable ice packs when the insects need to be held at low temperatures.

The importation of any living insects is usually controlled to some extent by plant-protection authorities of the importing countries. Permission to import live insects is granted only to responsible agencies who can demonstrate the safety of procedures being used. Frequently, export or import permits, or both, and appropriate documentation must be attached to the waybill or labeled to the packages. Containers should also be labeled with suitable cautions against extreme temperatures, such as exposure to frost or sun, and the cautions should be entered on air cargo waybills. When possible, overseas shipments should be timed to arrive at their destination on weekdays, to help reduce mortality of the insects because of delays in delivery outside regular office hours.

Insects can be shipped at any stage. There is little chance that they will develop significantly in their life cycle during an air transfer unless they are changing, or about to change, from one stage to another at the time a shipment is made. Predators are normally transferred as adults collected from the field or after feeding has been completed. Parasites are sent in host material, a certain proportion of which is parasitized, or as adults, cocoons, or puparia. Shipment of parasite adults removes the dangers of host and hyperparasites escaping. There is an added advantage in providing only the species that the recipient wishes to receive. However, more rearing and processing is required by the collecting agency, and adults are generally more susceptible to adverse shipping conditions. But perhaps the greatest disadvantage is the difficulty of synchronizing the receipt of parasite adults with the presence of susceptible stages of the host insect in the field or with the availability of suitable stages for laboratory propagation of the parasite; this can be done more readily with immature stages, by hastening or prolonging their storage at low temperatures prior to exposure to conditions at which they will recommence development. Also, communications are more easily effected over shorter distances, i.e., between a quarantine laboratory and the final recipient.

Most parasite and predator adults require food after 2 or 3 days. Honey or honey mixtures will provide the necessary nutrients and water; this can take the form of honey streaks, honey–agar droplets, or excelsior impregnated with honey. In closed containers, honey mixtures will also maintain certain humidities.

Information should be enclosed with each shipment, giving at least the following details: name and number of parasites, predators, or parasitized host species; host and plant from which collected; collection locality; dates collected and shipped; and any relevant references, data, or rearing suggestions that the collector can provide from his experience that will aid the consignee in handling and rearing the material.

If possible, material is sent in a series of small shipments rather than as a single large shipment; this minimizes the danger that all insects will perish because of a chance delay or unusually adverse conditions and may also allow adjustments in packaging or scheduling, which will reduce mortality in the later shipments. The consignee should be alerted as early as possible as to when shipments will be sent, how they will be routed, and, if possible, when they will arrive. This information will enable arrangements for quick delivery and for preparations for processing and rearing the imported material. Cablegrams are often necessary. The consignee should acknowledge each shipment immediately on receipt, noting the time of arrival and condition of the insects. This is particularly important when a series of shipments is anticipated and often should be done by cablegram.

QUARANTINE OF IMPORTED PARASITES AND PREDATORS

Insects imported from other countries must be adequately quarantined until they have been approved for release. This involves a thorough knowledge by the researcher at the quarantine station of both the taxonomic identities and the predacious or parasitic habits of the insects. The former is fundamental to any research practice; the latter is necessary to prevent the introduction of species that might prove harmful rather than beneficial. Errors cannot be allowed. Once an insect has become established, its removal is virtually impossible; there are also great dangers in handling possibly harmful strains and species of pests. Consequently, maximum precautions must be taken at all times.

Quarantine is essentially a system of regulations designed to prevent the escape of insects, although it may also be important to inhibit the entry of species that might contaminate cultures. There are two main avenues of escape from a building or its facilities: through windows, doors, or ventilators; and on the clothing of persons entering and leaving the quarantine premises.

The building used for the receipt and quarantine of imported insects must be of insect-tight construction, with particular attention to light and air ventilation systems that are necessary for rearing or propagating the entomophagous species under suitable controlled conditions. Insects should be confined in cages or other containers to reduce further the opportunities for escape. A closed-air ventilation system is advisable, particularly if the insects being handled are small enough to pass through fine screening. Facilities for fumigation and incineration should be provided within the quarantine premises for treatment of shipping containers and cages, which might be infested by undesirable insects or related arthropods. The positive phototropic reaction of many insects can be utilized by light traps and light-switching arrangements that attract them away from exit doors.

The more thorough the investigations abroad, the less need for investigations in the importing country. The most obvious advantage of studies of insects in their native habitat is the freedom to make observations without quarantine. This is particularly important when a species cannot be manipulated under artificial laboratory conditions and must be studied in a field habitat to ascertain its parasitic behavior. If time or facilities abroad limit such work, it must be undertaken, with great caution, in the importing country. The inherent difficulties involved require the utmost ingenuity from personnel responsible for propagation. Not only must the workers monitor cultures to adjust procedures at the first indication of malfunctioning, but they must perform this function within the limits of quarantine procedures.

Only essential personnel should be allowed in a quarantine area, and these workers should be fully aware of the dangers involved and the precautions to be taken. The extent of the precautions will often be dictated by the nature of the operations. A common regulation requires removal of laboratory coats before leaving a room or building.

RELEASE AND ESTABLISHMENT OF IMPORTED PARASITES AND PREDATORS

After assurance has been obtained that an imported organism is beneficial (i.e., that is has no undesirable primary habits and that it is free from hyperparasites and pestiferous potentials), production is initiated in the insectary to obtain sufficient quantities of adult forms for field establishment. Rarely is it possible to bypass the insectary-rearing process. Occasionally, however, direct shipments of parasite or predator adults can be arranged from the land of origin with complete assurance of the required safety necessary for direct release, and in some cases the insectary-rearing programs may be discontinued at a very early stage because field establishment can provide a substitute source of the organisms for redistribution. Emphasis, then, is generally placed on obtaining early field establishment of an exotic species with a fraction of the first available stocks, so that the laborious insectary-culture procedures may be discontinued as soon as possible.

The general rule, however, is to plan for an insectary-culture program with study emphasis on the biology of the natural enemies as related to field performance and synchronization of their release with the seasonal biology of the hosts. The study should include such features as adaptations to alternate hosts, tolerances to temperature and humidity, and the factors favoring mating, sex ratio, longevity, and oviposition of the species under differing conditions. Although some of these activities may be predicted largely on precedent information obtained from the foreign collector, from quarantine handling procedures, and from experience with closely allied species, the accurate determination of the habits, responses, and biologies of a newly imported species should constitute an integral part of the rearing program.

When rearing begins, the host used is ordinarily the one for which control is desired, so that habitual rather than casual or accidental relationships to that host can be accurately established and possible cryptic races of the natural enemy or host can be recognized. Aside from poor climatic adaptation or accidental relationship to the host, the acquisition of unsuitable racial characteristics by either the natural enemy or the host is the most prevalent cause for failure of transplanted parasites or predators.

Since both the general productivity and the host range of a parasite or predator species being reared under insectary conditions are often extended beyond the normal limits of that species in nature, unnatural hosts (sometimes called factitious hosts) are often most advantageous for insectary culture of the insect. In this respect, the primary concern is for ease of culture of the host insect and its abundant production on simple media, preferably nongrowing. Factitious hosts may often, therefore, be chosen over the natural host species on the basis of their adaptability for development of the parasite or predator on nongrowing synthetic or artificial media or on a storable plant product. In any case, handling problems will vary with the degrees of polyphagy of the natural enemy as well as those of the host, and all the difficulties encountered with respect to the parasite's adaptation to its hosts can never be completely anticipated.

Technological handling problems such as maintaining optimum insectary environments for mating and reproduction, or avoiding the contamination of stocks with disease organisms or dominant competitors, are normally expected, and success under such circumstances rests largely on the ingenuity of the propagator. Despite the most intensive preparation, conditions of obligatory diapause or other circumstances leading to unsynchronization of host–natural enemy relationships can defeat the best plan of propagation and necessitate consideration of an early field-release program, if only on a limited scale. The trend is toward greater concentration on appropriate colonization processes, with less emphasis on insectary culture. This policy has also been a normal outgrowth of the practical realization that the natural enemies destined to be most effective usually establish most easily and demonstrate their efficiency most rapidly. The policy of direct release has been further favored by the relative ease and security with which exotic natural enemies can now be transported by air in the adult stage without undue risk of hyperparasites or other contaminants.

Although procedural rules in some countries forbid importation and direct-release programs for natural enemies, if proper foundational information is acquired and proper care is exercised, direct release of screened air-transported natural-enemy adults is a realistic and modern alternative to the time-consuming and uncertain process of insectary rearing for colonization.

Insectary rearing of imported insects for field establishment usually involves concurrent handling of a number of species, since a sequence of parasites or predators is ordinarily desired. Time for full research under such circumstances is usually limited, and impressions of the merits of different species may be formed that are inconsistent with the final performance of the species in the field, where their reactions may be altered by climatic irregularities, dispersal habits, alternate hosts, and similar factors. These opinions are indicative of the empirical state of the present knowledge and the need for a more scientific basis for predictions of natural-enemy value.

A number of other insectary-culture problems connected with the propagation of imported natural enemies require scientific elaboration. Little is known, for example, regarding the possible loss of genetic diversity that may take place during insectary rearing from isogenic natural clones. The factors responsible for host suitability also are poorly defined, and additional research is needed in this area. The general nutritional requirements of various parasites and predators need much study if the rearing and culture of entomophagous species are to be scientifically advanced. Another research area of considerable significance in insectary culture of entomophaga lies in the elucidation of the factors contributing to the monophagous habits of certain parasites and predators and the evolutionary avenues through which host specificity develops in nature.

The culture of specialized phytophagous insects for weed control, the rearing of predator fish or mammals, or the propagation of insect pathogens for pest control involve specifically designed procedures.

Conditions conducive to establishment of imported natural enemies following their release in a new environment have been rather well determined from empirical trials, in which the factors attending success or failure have been carefully observed. The inability of an imported species to adjust to the climatic extremes of heat, cold, or aridity in its new environment is the most prevalent cause for failure of establishment. This is closely followed by host incompatability features, usually connected with the failure to recognize that the parasite attacks the host only because of its overflow from abundant reproduction on another more suitable host, i.e., an accidental host relationship, or because cryptic speciation leading toward incompatability of either the parasite or host has been acquired through isolation. Other common causes of failure are lack of necessary alternate hosts, inadequate food supplies for the adult parasites or predators, lack of seasonal synchronization of cycles with its host, and failure to compete with existing forms. Success has much more often attended the attempts to transplant organisms from temperate to tropical areas than vice versa.

Assuming that an intimate knowledge of the biological relationships of the natural enemies and their hosts has been obtained from previous rearing programs, it should be possible to predict with some exactitude from the preceding observations the most favorable conditions for establishment. The principal objective should always be to procure initial establishment in one area, from which natural spread and redistribution can be obtained.

Recognizing that few species of natural enemies are capable of controlling a host over its entire geographical range, a very few initial release sites are usually selected which might offer the best associations for both initial establishment and future spread. These are ordinarily kept at a minimum to avoid undesirable dilution of stocks, to provide more numerous sequential releases, and to permit more attention to the elimination of interference by competitors.

Colonization usually proceeds more readily under cages where competitors are excluded and where dispersal is minimized. Release in a field cage sometimes involves fumigating the cage and reinfesting it with natural enemy-free hosts. Some natural enemies invariably become established with releases of a few reproductive individuals, and others require high numbers. The contributing causes of such different reactions have not been established by competent research.

Natural enemies may become temporarily established and then fail to survive, so that only after the released species has gone through at least one complete season of climatic extremes is the permanence of colonization assured. A species may develop for a few years at almost explosive rates and later settle down to nominal rates of increase. Although this poorly explained phenomenon probably involves the accretion of adjusting competitor stresses, there may also be other conditioning factors operating to effect the new balance. All that is presently known is that the consummation of this effect may take up to 3 to 4 years on orchard crops, which is essentially the period required for a completely newly balanced ecosystem to be achieved after a serious upset of an existing balance on the same type of orchard trees when caused by disruptive chemical treatment.

The question is often posed of how long parasite or predator releases should be continued despite failure in establishment. Given proper release conditions, efficient species usually establish readily, and rarely do those most difficult to establish ever attain any degree of effectiveness.

Although it might be gathered from the preceding discussion, and from evolutionary inferences, that vital accommodation to a new host or to a new climate is commonplace among introduced natural enemies, this presumption has little basis in fact. Genetic plasticity among entomophagous insects seemingly operates within rather narrow limits. Accommodations seldom arise within short periods, other than those of natural selection from a broad gene pool. Preservation of the gene pool is of the greatest significance in rearing and release programs.

EVALUATION OF EFFECTIVENESS OF NATURAL ENEMIES

A biological-control project is not completed with the successful accomplishment of any one or any series of the processes outlined here, or even with the decline of the pest population to subeconomic levels. Insect populations normally fluctuate in response to a variety of naturally occurring stimuli; a decline in abundance, therefore, is often the result of causes quite independent of any actions taken with that objective in mind. Although such populations may cease to be troublesome for extended periods, if the basic situation remains unchanged, future population excesses can be expected.

Before biological control can be legitimately claimed, the influence of applied measures must be assessed, and cause and effect relationships between them and any population change must be demonstrated. This assessment can often be the most difficult part of a biocontrol project; it demands a continuing examination of population processes and a clear determination of the role of the manipulated elements. This task is rarely accomplished satisfactorily, and many of the successes claimed for biocontrols are quite unsubstantiated by acceptable evidence.

Too many biocontrol programs are conducted on purely empirical grounds. Often a variety of parasitic and predacious organisms are introduced concurrently, and success or failure of the introductions in the new community is noted. Most of these organisms simply vanish in the new environment, and no observations of their fate are possible. If repeated introductions do not result in establishment of an immigrant species, it is assumed that some essential element is lacking in the new environment, or that some feature of the new environment is antagonistic to the immigrant, and that the species is therefore unsuitable for colonization. Convincing evidence is rarely offered to substantiate this assumption.

Sometimes an immigrant species survives and reproduces in the new environment for a number of generations. The persistence of the new species is taken as evidence that it is killing pests, and thus some degree of host suppression must be taking place. If a measurable decline in the pest population follows, the introduced organism, especially if it is moderately abundant, is given credit for the decline, and a success is claimed for biocontrol.

It is unfortunate that large expenditures of time, labor, and money often fail to secure adequate pest control; but the number of such projects that have succeeded spectacularly more than justifies the total effort expended on the method. However, it is sad that they yield so little information about population processes and how they can be modified. The introduced species either survive or perish, and the pest population either persists or subsides, but how these events occur, or what cause and effect relationships may exist between them, is seldom established. Thus, the conclusion of one project, successful or not, does not materially aid in the persecution of another pest population by means of biocontrol. Since each project of this type must start from the same point and proceed down the same empirical path, the art of controlling pests biologically does not advance.

Fortunately, this type of project is less common now than just a few years ago. This is probably because of the development of a large array of organic pesticides by which pest situations can be contained during the period necessary for an adequate biological assessment. Before the advent of organic pesticides, the urgency of pest situations demanded that corrective measures be taken precipitously, with little time for investigation. Now, time may be purchased by the judicious use of pesticides, even though this procedure may complicate the biological situation.

Assessment of community processes begins with the preliminary investigation, at which time the initial situation is evaluated; it continues through the operational period, when the effects of applied measures are observed. It does not stop at this point, however, even though full economic control seems secured. An extended period of careful observation should follow, during which the continuing effects of the applied measures are assessed and their function in the newly established system is clearly demonstrated.

This task is made much easier if a consistent form of data presentation is established at the outset of a project. The life-table system seems the most appropriate yet devised for this purpose. Properly constructed life tables are appropriate to all stages of biocontrol projects and display the pertinent data in such a way that changes in the system are readily detected and can be subjected to meaningful analysis.

Although most entomologists admit the virtues of the biological method of pest control, they remain critical of how it is documented. They object to the testimonial and proclamation tactics formerly employed but fail to realize that these methods are rapidly being replaced with procedures for quantitatively measuring the true effectiveness of the natural enemies involved. The development of valid assessment procedures is admittedly far from complete, as momentary consideration of the necessary stipulations for acceptable proof of effectiveness will disclose.

Acceptable proof that a natural enemy has permanently reduced the general abundance of a pest species requires the following basic considerations:

1. All compensatory adjustments of the pest and natural enemy must have been completed prior to the assessment, so that the assessment measures only that increment of pest restraint that the natural enemy adds rather than replaces.

2. The evaluation must show a natural-enemy cause–effect relationship with a measured quantitative decrease in the average level of abundance of the pest, not just a change in the parasite numbers or in the parasite–pest ratios.

3. The measurement must reflect the true efficiency of the natural enemy under a variety of completely natural conditions of plant growth, climate, and pest and natural-enemy dispersal.

4. The evaluation should recognize that some natural enemies have a capacity to restrain incipient outbreak levels of certain pests, although they appear

to be incapable of suppressing the pest at higher density levels; i.e., they exhibit only a low host-density efficiency.

One useful procedure for completely fulfilling these stipulations for proper evaluation is the policy of comparing the long-term average levels of abundance of the pest, i.e., its steady density or equilibrium level before and after addition of a new biological control agent. This method can be and is being practiced with new importations whenever possible. The method, however, is patently impossible for evaluating the effectiveness of established or native natural enemies or for use in cases in which the urgent demand for biological control of a new pest forces natural-enemy introduction before the pest has acquired any degree of natural balance or stability. It is in these latter situations, however, that the greatest need has arisen for natural-enemy evaluation in recent years, and it is also in this area that great strides have been made.

A very short review of the technological methods devised to meet the demands for proper evaluation of native or established natural-enemy effectiveness follows, illustrating both the inherent difficulties to be overcome and the recent advancements and accomplishments. For convenience, the evaluation procedures are separated into the categories of correlation techniques, those utilizing natural-enemy exclusion, and those involving stochastic and mathematical models.

Correlation of Predator and Prey

The determination of population density–time curves for predators and their prey provides the main support for correlative procedures of assessing natural-enemy effectiveness.

Strong associative inference can be drawn from such census curves for a seasonal cause–effect relationship between the rise in abundance of a natural enemy and the decline of its host. Repetition of the effect, along with the typifying lag in natural-enemy numbers and a recognizably rapid decline in host numbers where the influence is from climatic or other nonregulatory factors, provides convincing evidence of the qualitative and quantitative effect of a particular biological-control agent. The procedure frequently separates the intensity of the various components in a complex of natural enemies, shows their seasonal or sequential influence for predictive purposes, provides a maximum of biological and ecological information, and has the advantage that it can be started at any time, with few difficulties other than development of suitable sampling techniques. The major objections are that it is subject to a variety of interpretations in the absence of a control and that it does not suffice to evaluate the effects of natural enemies that may have only a low host-density efficiency.

Although the preceding method is not completely adequate in itself, it is a most powerful tool when used in conjunction with other evaluation procedures. The refinement of this process into life-table data, i.e., survival-expectancy tables, not only spots the sequential effect in time of each mortality factor encountered, but also relates its interaction effect to precedent mortality influences, so that the critical impact of each factor can be better assessed.

These associative or correlative procedures are most valuable when combined with the results of various types of natural enemy-exclusion evaluation methods.

Parasite Exclusion Evaluation Procedures

Parasite exclusion evaluation techniques are designed to reproduce as far as possible the before and after natural enemy-introduction evaluation picture. They involve simply the removal of one or all of the natural enemies from the environment and the indirect determination of the effect of such removal on the host by the resultant increase in its numbers over that in a check where the natural enemies were untouched.

Mechanical Exclusion Techniques Mechanical exclusion techniques have involved the use of cages, barriers of sticky substances, air blasts, and even hand picking to exclude all or certain kinds of natural enemies. Each procedure has particular advantages for specific cases of evaluation, and many ingenious devices are available to avoid the most apparent disadvantages of each type of procedure. These methods adequately consider the possible effects of low host density-effective natural enemies, but they generally do not permit waiting for a new accommodative natural balance with all its compensatory adjustment before a final assessment is made of a changed level of average abundance of the pest.

An interesting modification of this technique was that of DeBach and his co-workers, in which ants were used to drive away the natural enemies of citrus scale insects.

Chemical Exclusion Techniques Frequent applications of a low dosage of certain pesticides affords a practical means of excluding natural enemies without seriously affecting the hosts and, indirectly, of evaluating the normal contributions of the natural enemies to the reduction of the host. Objections that pesticides may cause a stimulation of the host can be circumvented by treating an area surrounding the test block, so that in the course of their normal movements all the natural enemies are trapped from the test block without any insecticides ever having been applied to it. Chemical exclusion evaluation methods are particularly appropriate for use with situations in which the pests are of a type that does not cause complete destruction of the plant host, since here the main objection to this procedure can be surmounted, i.e., that the measurement is usually taken before a new stable balance has been established.

Despite the simplicity and apparent perfection of the chemical exclusion technique for natural-enemy evaluation—particularly when it is used in conjunction with natural-enemy–pest correlation procedures—the method has some defects. It cannot well separate individual components in a complex of natural enemies, and it can be assailed on the basis that trace quantities of the pesticide might in some unresolved way stimulate the fecundity or multiplicative capacity of the host insects. Research is under way to assess the validity of the latter criticism and also to develop specialized insecticide programs that will selectively eliminate certain natural-enemy species and not others, so that the separation of individual natural-enemy effects can be delimited.

Stochastic and Mathematical Models

The use of simulated models of field ecosystems has played a rather important role in making initial hypotheses concerning the relative efficiencies of various natural enemies. Although these models were usually so imperfect that they provided only the simplest of research guidelines, they still were most useful in exposing the potentials of individual species of parasites or predators. Now, however, with more-sophisticated equipment, such as bioclimatic cabinets and air-blast greenhouses for climate duplication, new possibilities for research are being opened in which the effect of an added or subtracted host-suppressant factor can be assessed under reasonably natural ecological conditions.

The recent adaptation of digital computers to the study of biological systems has provided the opportunity to develop the previously highly deductive processes of mathematical modeling of dynamic population processes into an inductive evaluation research procedure. With machine simulation of some of the simplest ecosystems, it may soon be possible to develop "if" games that can supply mathematical measures of the effects of the presence or absence of a critical natural enemy on a host population.

NATURAL ENEMIES

Most of the many thousands of insects and spider mites that attack crops, forests, livestock, and man occur in such low numbers that they never become pests of any consequence. There are many reasons for this, such as unfavorable climate or lack of alternate hosts, but we know that many potential pests are held in check by their natural enemies. Since all harmful insects are attacked by numerous parasites, predators, and pathogens, a pest may then be considered a species whose natural enemies fail to control it.

In agricultural environments, the community fabric may be under a severe strain, the cultural processes of man having come into severe conflict with the homeostatic forces of a natural community that would quickly dominate the site if cultural processes were withdrawn. In such situations, certain organisms gain ascendancy; they tend to be destructive to crops, and therefore they are pests. Other organisms, which in a natural community would regulate the pests, are in eclipse. These latter organisms offer the first opportunity for biological control. They possess these initial advantages: they are present on the site; they are probably well adapted to the general climate, the physical features, and the other endemic organisms of the community; and they possess the potential ability to regulate endemic pests under appropriate conditions. What must be sought are ways of providing these organisms with requisites permitting them to assume their regulative role within the community as it is modified by agriculture.

Features that influence the effectiveness of regulatory agents can be placed in the following categories: (1) intrinsic characteristics of the organism itself, e.g., reproductive rate, searching ability, physiological tolerances, genetic adaptability, mode of reproduction, ovarian development, oogenesis, and other inherent physiological processes; (2) intrinsic characteristics of the environment, e.g., climate, day-to-day weather, geological structure, geographic barriers, hyperparasites, predators, and pathogens; and (3) extrinsic characteristics of the environment, e.g., supply of shelters (from the elements and from enemies), supply of alternate or supplementary foods, alternate host, cultural practices of man, toxic elements in the form of pesticides, herbicides, fungicides, dust, air, water, and soil pollutants, and asynchrony of entomophagous and phytophagous populations.

A natural enemy fails because it is inherently inefficient or because its numbers are limited by some environmental factor. Four basic things can be done to increase the effectiveness of such beneficial insects: find and introduce a more effective species from elsewhere, change the genetic constitution of the species to overcome its limitations, modify the environment to make it more favorable, or collect or rear large numbers of the species and release them where they are needed.

The introduction and establishment of exotic natural enemies has already been discussed in detail. Selective breeding of better-adapted species is a technique that many authorities consider highly promising, but one that few have investigated. There have been no successful cases of control by parasites or predators deliberately modified in this way, but insects are genetically plastic organisms, and some of their important characteristics can be altered by selection. The host preference of *Horogenes molestae* (Uchida), a parasite of the oriental fruit moth, *Grapholitha molesta* (Busck), was changed by first inducing it to oviposit in the potato tuberworm, *Phthorimaea operculella* (Zeller), by the use of an attractant for 11 generations. After this, the attractant was no longer necessary, and selective breeding for 39 generations resulted in a strain that reproduced 24 times more efficiently than the original on the factitious host. In Canada, the temperature response of *Dahlbominus fuscipennis* (Zetterstedt), a parasite of the European pine sawfly, *Neodiprion sertifer* (Geoffroy), was changed in 4 generations. It was later found that virtually the same change had also occurred in the field, which suggests that in some cases natural selection may be as effective as artificial breeding, without the danger of inadvertently selecting for undesirable characters in laboratory rearing. In California, the response of the parasite *Aphytis lingnanensis* Compere to both high and low temperatures was altered.

MODIFYING THE ENVIRONMENT

To change the environment in favor of a natural enemy, it is necessary to know what factor or factors limit the insect. If the limitation is inherent, there may be very little that can be done about it. For example, laboratory investigations have shown that some parasites cease to attack the host when they have parasitized 40 to 60 percent of the population. However, many of the environmental factors limiting natural enemies can be overcome. These factors are almost always a short supply of resources, unfavorable weather, or mortality caused by secondary enemies or by man.

All parasites and predators require several resources in addition to the host insect that they use for food. Some of these, such as oxygen, are always present in abundance. Water can generally be obtained from dew, except in dry climates. However, supplementary foods and a suitable habitat in which to live are often absent or in short supply in the place where the parasite or predator must live in order to attack a given host effectively. For example, adults of many hymenopterous and dipterous parasites require food to lay eggs or to live more than a very short time. Some species find this food by feeding on the blood of the host insect in which they lay their eggs, but many others do not have this habit and can feed only on nectar from flowers or extrafloral nectaries. Such food must be within flight range of the host insect and must occur at a time when the adult parasite is present.

Supplementary food can sometimes be supplied by man. Thus, Russian workers have shown that the parasite *Apanteles glomeratus* (Linnaeus), which attacks two species of cabbageworms, *Pieris* spp., on cabbage and related crops, obtains nectar from mustard flowers and will live longer and lay more eggs if these are present. When quick-flowering mustards were planted in fields of cole crops, parasitization of the host increased from about 10 to nearly 60 percent. The Russians have also reported that planting the weed *Phacelia* sp. in orchards provides a source of nectar for *Aphytis proclia* (Walker), a parasite of the San Jose scale, *Aspidiotus perniciosus* Comstock, and that this practice results in an increase in parasitism.

Sometimes a place to live is a critical factor. For example, in North Carolina, several species of paper nesting wasps, *Polistes* spp., prey on the hornworms, *Manduca* spp., that attack tobacco. These wasps require a protected spot in brush or weeds to build their nests, and there is no such place in the fields of tobacco, corn, and cotton commonly grown in that region. Thus, unless there are fencerows or woods within a few hundred yards of a tobacco field, the number of wasps living within flight range will be much reduced. It was found that wasps would nest in small wooden boxes erected on posts around the edges of tobacco fields in the spring. Since the nests were close to the tobacco fields, the wasps tended to search for food there, and the number of hornworms killed was increased by about 50%, thus reducing the need for insecticide applications.

When weather is the factor limiting the numbers of a natural enemy, there may be very little that we can do about it. However, in many cases weather is a deleterious factor, because there is no shelter where the natural enemy can escape from the full effects of rain, heat, or cold. In California, the parasites of the spotted alfalfa aphid cannot tolerate the high temperatures that occur when alfalfa is cut. Consequently, if the whole field is cut at one time, numbers of the parasite are greatly reduced, but if the alfalfa is cut in strips, the parasites can find shelter in the uncut portions. The numbers of other beneficial insects were also greatly increased by strip-cutting.

The date when insect pests and their enemies become active in the spring, or inactive in the fall, is generally determined by the length of the day or by temperature. Natural enemies are often known to be ineffective because they are not well synchronized with their hosts. They may emerge too early in the spring or remain active too late in the fall and perish from lack of food when the host is not present. The natural enemy sometimes emerges so late in the spring that the host has a head start and reaches high population levels before the enemy can bring it under control; or the natural enemy stops activity too early in the fall and permits the host to build up high overwintering populations. Thus, the *Polistes* wasps attacking hornworms stop brood-rearing and, consequently, kill very few hornworms late in the season when the third generation of the pest is produced.

The parasite *Apanteles congregatus* (Say), which also attacks hornworms, emerges too early in the spring. In this instance, there appears to be very little that can be done to improve the situation, but in other cases it may be possible to provide the parasite with an alternate host to carry it over a period of shortage. In the Canete Valley in Peru, corn, flax, and other crops are planted to provide an alternate food supply for parasites and predators of insects attacking cotton. This practice, plus the elimination of insecticidal control, reduced the principal pest to innocuous levels within 3 years.

The natural enemies attacking pests are, in turn, attacked by secondary enemies, which may considerably reduce their populations. Very little research has been done to determine if the enemies of the enemies could be reduced, but there has been at least one successful experiment. In the Solomon Islands, the predaceous ant, *Oecophylla smaragdina subnitida* Emery, is an enemy of a plant bug, *Amblypelta coccophaga* China, a pest of coconut. Its colonies are eliminated by another ant, *Pheidole megacephala* (F.), where clean culture is practiced. In wartime, the neglected coconut groves developed a heavy undergrowth and were reoccupied by *Oecophylla*. Later, palm fronds were placed tip end up against the tree trunks so that *Oecophylla* might escape *Pheidole* predation. This practice resulted in control of the bug.

Certain cultural practices may greatly reduce the effectiveness of natural enemies. For example, many parasites and predators pass the winter in the debris on the surface of the ground. If the land is plowed before they emerge in the spring, only a few survive.

One of the most serious factors reducing populations of parasites and predators is the application of insecticides. In many instances, probably in most, the survival of beneficial insects can be increased by an integrated control program using selected insecticides and careful timing. These procedures are discussed in Chapter 17.

MASS PRODUCTION AND DISTRIBUTION

The populations of natural enemies attacking pests can be increased directly, either by collecting and redistributing natural populations or by mass-rearing and distribution of the insects. For example, the convergent lady beetle, *Hippodamia convergens* Guérin-Méneville, in California moves from the valleys to the mountains and congregates there in huge aggregations. The beetles are then collected and sold to organic gardeners or occasionally to farmers whose crops are attacked by aphids. There is little, if any, evidence that such releases are effective, but the principle will apply to other insects. Thus, in California, outbreaks of the cyclamen mite, *Steneotarsonemus pallidus* (Banks), in second-year strawberry fields is partly the result of a lag in the appearance of predatory mites. When clippings from older fields having both predators and prey were placed in new plantings, the natural balance was established earlier.

Workers in California have invented a large suction machine, which, when passed over a field, will collect millions of insects, both pests and natural enemies. There are various procedures by which the beneficial insects caught might be recovered and released in other fields where there are pest problems.

Mass-rearing and release of natural enemies have also been attempted in several cases. The egg parasites, *Trichogramma* spp., which attack many species of Lepidoptera, have probably received the most attention. Very large numbers of these parasites can be reared in a small space in the laboratory on the eggs of the Angoumois grain moth, *Sitotroga cerealella* (Olivier), and releases have been tested against a variety of pests. In most cases, the method has not been successful, but recent reports from Poland indicate that careful selection of the correct strain of the parasite and proper timing of releases controlled the plum moth, *Laspeyresia funebrana* Tr., as well as did insecticides. A predator, the green lacewing, *Chrysopa ploribunda* Fitch, is now being mass-produced in California and can be purchased at a cost of $1 per thousand eggs. It has been shown that 500 eggs dumped into the crotch of a pear tree will control the grape mealybug, *Pseudococcus maritimus* (Ehrhorn), for 2 years. In this instance, control is not considered practical, because insecticides must still be applied against other insects.

In some experiments, attempts have been made to control pests by repeated releases of natural enemies in the same crop season. There are apparently no cases in which this method has proved practical with parasites and predators, although pathogens can be used in this way. Repeated releases of parasites and predators may be effective but will probably be more costly than insecticides. However, if natural enemies could be released at the beginning of the active season and would multiply in the field, one release might be effective and considerably more economical than repeated applications of an insecticide.

There are many parasites and some predators capable of reproducing faster than their hosts and of bringing the pests under control eventually, if there is sufficient time, but they are prevented from doing so by a combination of a short active season and high mortality during the remainder of the year. If a natural enemy suffers heavy losses from winter weather, too early emergence in the spring, plowing of the land, or some other cause, its numbers in the spring may be too low for it to subdue the host during the summer. Such an enemy might be very effective if its population were increased by supplementary releases.

One possible problem in mass production and distribution is the selection of an effective parasite or predator. Experiments on mass release have mostly used parasites or predators that could be easily collected or reared, and these may or may not have been the most effective species. For example, some experiments on the mass release of *Trichogramma* in cotton and sugarcane fields have been conducted with a species whose preferred habitat is in orchard or other types of trees.

Most pests are attacked by at least five or six different natural enemies, and, since the production of sufficient numbers of the beneficial insects for field tests may require a considerable investment in research, the available species should be screened to select the most effective ones before large-scale rearing is attempted.

The chief requirements for mass release are apparently as follows: (1) the natural enemy must be able to find the host on its host plant and in its habitat, and remain there; (2) it must be able to live and perhaps reproduce under the prevailing weather conditions; (3) it must be able to attack the host at the density prevailing at the time of release and reduce it below the economic threshold or prevent increase beyond that level; and (4) there must be economical methods of rearing and distributing the species in sufficient numbers.

To select the most suitable parasite or predator from several that may be available, it will be necessary to measure the above variables and perhaps others as yet unidentified. Some of the variables, such as suitability of the host or rate of reproduction under prevailing weather conditions, can be determined in the laboratory with more or less standard procedures. However, it will be necessary to devise new techniques and procedures to measure some of the other characteristics.

For example, fewer natural enemies would normally be required for release when the pest population is very low than when it is high, but some parasites and predators do not operate efficiently against low host densities. Some coccinellids, for instance, simply fly away if food is too difficult to find. If predacious larvae that can move only short distances are released, they may search for other sources of food and neglect the pest. These reactions can be tested in the field, but the procedure requires very large areas and the release of huge numbers of test insects. To select one species from many by field tests might be too costly. However, laboratory tests to determine reactions to host density may be misleading, since insects in cages may react abnormally. The problem can undoubtedly be solved by further research.

Another unsolved problem is how to select natural enemies inherently capable of giving a high degree of control. In laboratory experiments in which varying numbers of parasites were tested against a fixed number of hosts, the number of hosts killed increased as the number of parasites increased, but there was always a point of saturation where large increases in the numbers of parasites killed very few additional hosts. This point varied greatly between species. For example, in certain experiments with *Trichogramma evanescens* Westwood and the Angoumois grain moth, the maximum practical level of control was about 95%, but, in another experiment, with *Trachyophytus inornatus* (Pratt) on the beet webworm, *Loxostege sticticalis* (Linnaeus), it was only about 50%. It is not known whether or not such differences would occur in the field or how to conduct screening tests in the laboratory.

One of the reasons for the apparent failure of biological control methods in some tests is that the methods have been applied in too small an area. All parasites and predators have some ability to disperse, and some of them normally move considerable distances. Because of interplot movement of the insects, standard experimental techniques using small plots in the same field, or even whole fields, may be practically worthless for testing biocontrol measures. Presumably, treatment would increase the number of natural enemies in treated plots and decrease the number of hosts. Since emigration of either will be greatest where numbers are highest, the natural enemy will tend to move from treated to check plots, and the host will tend to move in the opposite direction, thus violating the basic assumption of randomness necessary for statistical analysis, and causing the experimenter to underestimate the effect of treatment. Furthermore, ecological studies have shown that reproduction and mortality are nearly in balance in some pest populations. If it does not interfere with natural control, a comparatively small increase in the death rate may be enough to cause a gradual but serious decline in the mean level of pest abundance. This effect cannot be determined in small areas, because the experimental population is continuously replenished by immigration.

A case in point is provided by a long series of experiments with light traps used against the tobacco hornworm, *Manduca sexta* (Johannson). When traps were placed around single fields, the reduction in populations of the pest was about 14%—too little to be of any value. Then studies of dispersal showed that hornworms frequently moved 3 or 4 miles in a single night. When traps at the rate of three per square mile were spread over an area of more than 100 square miles, and cultural control increased, the reduction at the center of the area was 60 to 80%. As a result, the use of insecticides in the area with light traps has been practically discontinued for the last 5 years. Thus, an investigator who applies his treatments to small areas may wrongly conclude that a method is worthless, and, unless he studies the dispersal pattern of the pest and its natural enemies, he may never suspect his error. In many cases, perhaps in most, biological control by mass releases cannot be adequately tested, nor will it be fully effective, unless it is applied to an isolated population or a very large area. The cost of such large-scale experimentation is another reason why methods of conducting accurate preliminary screenings are essential.

If it appears that a particular species of parasite or predator would be suitable for mass release, the problem of rearing sufficient numbers for field tests should not be too difficult. Almost any parasite or predator can be reared in the laboratory in small numbers on its natural host, but the host may in turn require a plant for food. If an attempt is made to rear large numbers, the production of plants may require a prohibitive amount of space in the greenhouse or laboratory. It is possible that some natural enemies could be produced on hosts living on plants in the field, but this has not been attempted on a large scale. In most of the successful cases of mass production of natural enemies, the host insects were reared on stored grain or on a storable plant product. For example, the mealybug destroyer, *Cryptolaemus montrouzieri* Mulsant, was successfully produced in very large numbers in California by rearing the host mealybugs on potato sprouts. In many cases, the host used for rearing was different from the target species. It is possible that a parasite or predator reared in this way may change its host preference and be less effective than if reared on the host it is expected to attack in the field.

In recent years, the production of host insects on synthetic or semisynthetic media has made great advances. The screw-worm fly, *Cochliomyia hominivorax* (Coquerel), was produced by the hundreds of millions on cheap meat. Some millions of tropical fruit flies have been reared on diets consisting mostly of dried carrots. Several other insects, for example, the cabbage looper and the boll weevil, *Anthonomus grandis* Boheman, are now being produced on a pilot-plant scale on artificial media.

Since the basic dietary requirements of all the insects studied, including parasites and predators, are chemically very similar, it should be possible to produce some beneficial species directly on artificial diets. This has already · been done for a few species. For example, the dipterous parasite *Pseudosarcophaga* n. sp. [*Agria affinis* (Fallen) of authors] was mass cultured in Canada on liver and fish. Coccinellid beetles, which are predators of aphids, grow quite well on a diet of dried aphids and water. Suitable aphids might be collected in very large numbers from alfalfa fields, but it seems more practical to find substitute ingredients.

If a method of rearing is available, there is the additional problem of distributing the insects in the field. In the case of the screw-worm, this problem was solved by designing special types of boxes to contain the insects, and special machinery for dropping the boxes from aircraft.

Manipulation of the environment or mass release of natural enemies offers many advantages over control by insecticides. There are no toxic residues and no contamination of the environment, and thus no hazard to the health of man, to other beneficial insects, or to wildlife. In some cases, biocontrol methods may be cheaper than conventional control measures. For example, the Russian technique of planting a few mustard plants in cabbage fields to increase the effectiveness of parasites of cabbageworms would be considerably cheaper and less troublesome than the repeated application of insecticides.

However, biocontrol methods also have some disadvantages. The fact that natural enemies tend to be highly specific and do not interfere with other beneficial species makes it necessary to apply other control measures against other pests that may be present at the same time on the same crop. Another disadvantage of these methods is that they require an extensive knowledge of the pest and the factors determining its abundance. The research needed to obtain this information is more difficult and takes more time than is normally required for the use of pesticides. This precludes the application of the methods in emergency situations. However, for the solution of long-standing pest problems, where the continuous application of insecticides is both expensive and a source of much difficulty with insect-pest resistance to insecticides and undesirable residues, research on more permanent and less troublesome methods of control will probably be less expensive than the continuous investigation necessary to develop new and improved pesticides.

Biological control has sometimes been highly effective, especially in those cases where an introduced natural enemy has reduced a pest to innocuous levels with no further effort required. More often, however, the use of natural enemies merely reduces pest populations without giving completely adequate control, and insecticides or other methods are still necessary. For this reason, biological control methods are often rejected by entomologists and farmers, despite their many advantages.

There are, however, certain theoretical considerations indicating that the use of biocontrol methods in conjunction with insecticides or other procedures may be more effective and less costly than the use of any one method alone (see Chapter 17).

COMPETITIVE DISPLACEMENT

The ecological principle of competitive displacement between ecological homologues encompasses cases where one species of insect or other organism has displaced or eradicated another species in nature over more or less extensive areas. Although Darwin may have had ideas relating to the principle, the first clear statements concerning it seem to have been put forth by Grinnel at Berkeley, California, as early as 1904. Mathematical analysis of simple models commenced in the 1920's, and Gause published the first experimental demonstrations in the early 1930's. As a result, the principle is sometimes referred to as Gause's law. This principle has not yet been purposely applied by man for eradication or control of pests, but it undoubtedly can and someday will be used successfully. It will not be a principle of broad application to all or even most pest species. Just as the use of the sterile-male technique for eradication or control presently applies to only a limited number of suitable species, so it is with competitive displacement. However, assuming an ideal hypothetical case, competitive displacement can be brought about with a minimum of cost and effort, and actual eradication can result. Success with even one major pest species would be an outstanding achievement. A broad review of this entire subject may be found in the *Annual Review of Entomology for 1966*, pages 183-212.

THE PRINCIPLE

The principle of competitive displacement is based on the result of competition between species for identical or virtually identical requisites in the same habitats. It has been described as involving different species having identical ecological niches (that is, ecological homologues) that cannot coexist for long in the same habitat. In other words, one will eliminate the other sooner or later.

To understand the definition of competitive displacement clearly, the terms used in it also must be precisely defined. "Ecological niche" refers to the role played by an animal (insect) each of which is distinctive in its precise food, spatial, or habitudinal requirements in a particular habitat. What an animal (insect) does and what it needs as requisites for survival and reproduction in a given habitat determine its ecological niche. Note that "niche" as used here is in no way equivalent to habitat or microhabitat. If individuals of different species have truly identical needs for food, shelter, and other requisites in the same habitat, they have identical niches; they are ecological homologues and one will displace the other. From a practical viewpoint, only one requisite, such as food, need be an identical requirement for two species in the same habitat in order for competitive displacement of one by the other to occur. One or more of their common needs must be exactly, not superficially, the same. For example, insect species feeding on different parts of a plant, such as one on fruits, the other on leaves, are not ecological homologues and may coexist.

The operation of the principle is simple, even though it remains a controversial issue among some ecologists. It ultimately rests on the idea that no matter how closely related and how nearly exact in needs and habits one species may be to another, their genetic constitutions will be different and one of the species will have an advantage, i.e., will be the "fittest" in a given habitat. Competition between the two will result in "survival of the fittest," just as it does in natural selection and evolution. The winner will be the species producing the most female progeny which survive to reproduce, per parental female per unit of time. This is a simple mathematical truth, although the time required for completion of the process may be short or long, depending on the degree of effective reproductive advantage one species has over the other.

Competition between ecological homologues need involve merely the attempted or actual utilization by the two species of common essential resources, or requisites. Direct harm, aggression, interference, or bother need not be involved for competitive displacement to occur, although such processes may influence the outcome by modifying effective reproductive rates. However, competition may involve only a purely passive search for and utilization of the same food by each species, without one paying any attention to the other. Many ecologists consider that food must be in short supply in order for competition to occur, but this view is not held here. It is assumed that an apparent abundance of food or other requisites does not preclude the occurrence of competition and competitive displacement. Even with an abundance of food which is a common requisite for two ecological homologues, one species will eventually displace the other, just as a superior genetic strain of a species will ultimately replace an inferior one, even in the continued presence of surplus food. This has been demonstrated experimentally and has occurred between pest insects in the field.

EXAMPLES OF COMPETITIVE DISPLACEMENT IN NATURE

There are many recorded cases where one species of insect or other organism has, or appears to have, replaced or displaced another species in nature. Often, such cases are not sufficiently well documented or studied to ensure that competitive displacement between true ecological homologues has occurred, but this appears to be the most likely and frequently the only explanation. Several cases in the field have been thoroughly studied in which competitive displacement between ecological homologues has taken place. Also, many cases have definitely been demonstrated in laboratory studies, particularly with competing species of stored-products insects.

Cases of competitive displacement recently reviewed in the literature include, among many others, displacement between two species of scale insects of the genus *Aonidiella* in California; between the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), and another fruit fly, *Dacus tryoni* (Froggatt), in Australia; between *C. capitata* and *D. dorsalis* Hendel, in Hawaii; among three species of *Aphytis*, which are parasitic on the California red scale, *Aonidiella aurantii* (Maskell), in California; and among three species of *Opius*, which parasitize *D. dorsalis* in Hawaii. In all these studies, some of which are not final, a well-established species has been displaced and essentially eradicated from a good portion, or perhaps all, of its former range in the area studied. There would now seem to be very little reason for not accepting competitive displacement between ecological homologues as an established and demonstrable valid ecological principle, although many questions remain to be answered with respect to details of particular studies or observations.

The foregoing examples involved cases that were studied while the displacement process was going on. Another "type" of competitive displacement, by far the most commonly available for study and analysis in nature, involves the end result of the process, which leaves two allopatric species populations with a narrow band of overlap between them. One displaces the other from its territory and vice versa because one has the advantage in one habitat or zone whereas the other is the winner in a slightly different habitat, even though either could do well if it occurred alone in both habitats. This has been termed "mutually exclusive distribution" and points up the fact that competitive displacement of one species by another is not an inherent species characteristic alone, but is influenced by environmental conditions. Thus, from a practical viewpoint, we must recognize that displacement may occur in one habitat but not necessarily in another. That is, a species may be displaced from all or only a portion of its original range by an ecological homologue.

POSSIBILITIES AND PROCEDURES AS APPLIED TO PEST INSECTS

How might the competitive-displacement principle be applied for control or eradication of pest insects? Obviously, no one wishes to risk the possibility of trading one pest insect for another that is as bad or possibly even worse. Utmost care and judgment based on sound ecoloigical study and principles would have to be applied just as they have been in the use of purposely imported plant-feeding insects for the biological control of weeds. Especially suitable cases would have to be chosen and these would be restricted to a limited number of pest species. However, the distinct possibility of eradication or great reduction in the population of even one major pest insect from an appreciable area would justify a large amount of research and field experimentation.

The first trials should, and undoubtedly will, involve the importation and colonization of an ecological homologue, which itself is not a pest, for displacement of a pest. Several more or less hypothetical possibilities follow for illustrative purposes.

The house fly, *Musca domestica* Linnaeus, has a number of competitors in nature for the larval medium. If the adults of these competitors have habits different from the house fly, so that they do not invade dwellings or otherwise act as pests, then it would appear logical to attempt to utilize or manipulate one or more of them to bring about competitive displacement of the house fly. Mass production and periodic colonization of certain species might be necessary to accomplish this in certain habitats or to speed the process of displacement. This would have to be determined by experimental trials. A possible case in point may be illustrated by the rather innocuous stratiomyid fly, *Hermetia illucens* (Linnaeus), whose larvae have eliminated house fly larvae in limited field tests, apparently as a result of competition for common food. Others among the many known coprophagous species might provide more-suitable possibilities for competitive-displacement trials. This illustration emphasizes the point that competitive displacement may be brought about by competition between immature stages of different species as well as between adults. Furthermore, competition does not have to be for food; it can be for space, shelter, or other requisites.

Virtually all insects that constitute pests only in the adult stage, but whose immature stages are aquatic or soil-inhabiting, should be suitable subjects for competitive-displacement trials. Mosquitoes, eye gnats, biting gnats, and certain biting flies are some likely possibilities. Mosquitoes and other forms that are pests of humans might be eliminated or greatly reduced by the importation and establishment of an ecological homologue whose adults do not bite humans but whose larvae are ecological homologues in the aquatic habitat. Also, a vector of disease pathogens might be replaced by a nonvector. Even though the nonvector might bite humans, eradication or reduction of the disease would be the major consideration.

Competitive displacement can be direct, as a result of importation and establishment of a competitor, or it can be indirect, as a result of habitat manipulation, as illustrated by the work of Aitken and Trapido in Sardinia. These workers showed that after 2 or 3 years, classical eradication attempts against *Anopheles labranchiae* Falleroni, a serious mosquito vector of the protozoan causing malaria, led to another previously rare species, *A. hispaniola* (Theobold), becoming common and dominant while *A. labranchiae* became scarce. The newly dominant species, *A. hispaniola,* however, is not a vector of the malaria-producing organism. This replacement apparently occurred because of differences in habits of both adults and larvae between *A. hispaniola* and *A. labranchiae,* which favored relative survival of the *A. hispaniola* population under the eradication measures employed. Had this program been continued, it appears quite possible that *A. labranchiae* would have become eradicated, but not from the attempted eradication measures alone—rather from the competitive advantage (reflected by more surviving progeny per female) conferred on *A. hispaniola* by those measures.

Along more direct lines, Bierne suggested that biting flies might be eliminated from a locality by introducing from another part of the world a species that does not bite man (or domestic animals) but that has virtually the same habits and ecological requirements and displaces the biting species when the immature stages of the two compete in the same habitat. Certain eye gnats of the genus *Hippelates* might be handled similarly. The adults of some species are pests of humans; the adults of others are not attracted to humans. If, among the latter group, species could be found whose larvae were ecological homologues of the larvae of a pest species, then competitive displacement of the pest species would be a real possibility.

When competitive displacement of phytophagous pests is considered, the problem becomes more complex because of the greater potential hazards involved. Quarantine officials will not look with favor on the importation of an ecological homologue that is a potential pest in order to eradicate an already established pest. However, we should not decide blindly that there are no possibilities in such an approach against phytophagous pests. Admittedly, they will be few and highly restricted to specialized cases. Again, this is similar to approaches and techniques in the biological control of weeds, where potential hazards and conflicts of interest are weighed against potential gains. Extremely serious pests may justify extreme measures, provided that sound consideration, study, and experimentation have furnished an adequate scientific basis for proceeding.

Insect vectors of plant-disease organisms may offer especially suitable targets for competitive displacement. They may occur in relatively low numbers that result in no direct economic crop damage; transmission of the pathogen results in the injury. Logically, they could be replaced by an ecological homologue which is a nonvector, and the nonvector would then exist in numbers too low to cause economic damage. Should an insect vector overwinter on an obligate alternative wild host plant, an even safer procedure might be possible. Use of a nonvector ecological homologue that was restricted to the overwintering wild host plant could result in elimination of the vector. In cases where more than one alternative host plant was used by the vector, the degree of displacement would depend on how closely the nonvector duplicated the host plants of the vector. The beet leafhopper, which transmits the curly top virus of sugarbeets, might be considered as an example. It overwinters in California to a large extent on the weed Russian thistle. Importation and establishment of an ecological homologue restricted to Russian thistle could greatly reduce this problem.

Another approach would be to use an imported ecological homologue that is a potential pest, for competitive displacement of a phytophagous pest, if, for example, the imported homologue could not survive the winter. Periodic colonization of large numbers of the imported species during favorable periods of the year could be used to displace the original pest. The imported species would die out later when colonization was terminated, because it could not survive the winters.

Another possibility might be the displacement use of an imported ecological homologue that is a potential pest but is known to be subject to biological control, whereas the original pest was not. The Florida red scale, *Chrysomphalus aonidum* (Linnaeus), might fit this category. It has been brought under successful biological control during the past few years in every country into which its parasite, *Aphytis holoxanthus* DeBach, has been imported and colonized. The purposeful importation of Florida red scale into a new country could lead to the replacement of another species, such as dictyospermum scale, *C. dictyospermi* (Morgan). After displacement was complete, the parasite of the Florida red scale would be imported for biological control of that scale.

A previously unrecorded case of this sort has apparently occurred naturally in the interior citrus counties of southern California during the past few years. It is not well documented, but a former pest species actually has disappeared completely as far as we know, so the story of the probable chain of events may be apropos. Previously, the two species of soft-scale insects, the citricola scale, *Coccus pseudomagnoliarum* (Kuwana), and the brown soft scale, *Coccus hesperidum* Linnaeus, occurred together in citrus groves in various areas. Both were accidental importations that had been established for many years. The citricola scale did not have nearly as effective natural enemies as did the brown soft scale and thus had a competitive advantage. Citricola scale was an important pest, but brown soft scale was not. When parathion and malathion became common and were in general use during the 1950's, citricola scale was easily controlled chemically but brown soft scale was not, although its parasites were destroyed. As a consequence, brown soft scale frequently rose to pest status, but citricola scale became scarcer. This marked a reversal of competitive advantage and was eventually followed by the apparent complete disappearance of citricola scale in the field.

Another possibility could involve the competitive displacement of one species not subject to any known eradication procedures with another species that has been subject to eradication in other areas. After the original pest species had been completely replaced by the imported homologue, the latter could be eradicated by a known safe method, such as the use of sterile males. This approach might be considered for various fruit flies (Dacus, Ceratitis, and Anastrepha).

There is an obvious apparent drawback connected with the preceding hypothetical examples. We could not afford to permit two phytophagous ecological homologues to compete unchecked. Damage to crops or other valuable commodities would preclude such an approach. However, the use of insecticidal control is compatible with the competitive-displacement process. The two competing species could thus be maintained below economically damaging levels, yet displacement of one by the other could still occur, although at a reduced rate. This has not yet been proved by practical evidence, but laboratory experiments have demonstrated it, and field observations apparently confirm it. Thus, theoretically at least, the use of combinations of all the previously suggested manipulations of ecological homologues with interim chemical-control measures to eliminate economic damage appears feasible.

It is extremely difficult to identify the specific benefits of basic research in biological-control programs and, even in the best of circumstances, to justify basic research simply by identifying where it has enhanced applied programs. The knowledge behind any application of science has a number of interrelated sources in basic research, in empirical and applied studies, and in intuitive judgments based on common sense and the community wisdom. It would be difficult to unravel such a complex net. It might even be harmful to do it, for such action leads too easily into a simplistic trap of weighing the merits of basic research by the number of specific improvements of application. The value of basic research often lies in providing a general rationale or in suggesting what not to do. Basic research can, in short, set the boundary conditions for possible action.

The role of basic research in the biocontrol of insect pests can therefore be best assessed by comparing the essential features of available basic constructs with the prime characteristics of the real world. If the basic constructs are not concerned with a significant number of the essential characteristics of nature, then inadequate boundary conditions are set and erroneous actions suggested.

Any applied program can draw on basic information from a large number of different disciplines. Biological-control programs rely on taxonomic studies to show the species of natural enemies suitable for introduction; on nutritional and behavioral information to identify weak links in the life history of a pest; on suggestions of different ways to transport and culture predators, parasites, and pathogens; and on physiological studies to demonstrate climatic tolerances of specific natural enemies. Although all these studies provide extremely useful information, the central source of basic information for biological control lies in research on population processes and their interactions.

POPULATION BIOLOGY

Populations, like most organized systems, are generally characterized by stability. Very often, it is only when this stability is grossly disrupted that the population comes in obvious and direct competition with man for a commonly shared resource—an extremely rare event in relation to the large number of species of organisms. The remarkable stability of populations has been considered by most population biologists to be the result of the action of homeostatic or negative feedback mechanisms that resist change. Any departure from a norm tends to be opposed, and opposed with increasing vigor as the departure becomes greater and greater. A parasite, for example, can cause an increasing proportion of deaths in a population as host density rises above a certain value and can relax its effects when densities decrease below this value. As a result, there is a continual tendency for densities to stabilize around one particular level.

In practice, however, these feedback processes never act so simply. First, there are some agents that act in the opposite way, as positive rather than negative feedback mechanisms, and these encourage or accelerate departure from a norm. Any agent, for example, that causes a constant number of deaths, irrespective of density, would act in this manner, for the proportion destroyed and the population effect would decrease as density increased. Second, other agents destroy or affect a constant proportion of the population over wide density ranges, and while this action can profoundly affect the density of populations, it cannot by itself regulate the numbers of animals. Some aspects of climate are often cited as operating in this density-independent manner. Third, while some agents react immediately to a change in the density of a population, others react only after a considerable delay. As an example, the inevitable lapse in time between an event leading to the birth of a predator, and its appearance as an active mortality agent, produces delays of profound consequence in homeostatically regulated systems. Thus, although individual predators can immediately increase their rate of consumption of prey that increase in density, any resulting increase of predator density is not felt until the next generation. Thus, the magnitude of predation at any moment is partly determined by responses to conditions at previous moments. This tends to produce instability by generating oscillations in numbers of high magnitude or progressively increasing magnitude. The same kind of instability is seen in economic systems that can generate extremes of inflation and depression and in certain "disease" conditions of animal and machine that result in wildly oscillating behavior. Wherever it occurs, the instability can be damped by negative feedback mechanisms that act with no delay—mechanisms that have recently been discovered as part of the attack behaviors of parasites and predators.

The preceding discussion presents, in a very condensed form, the essential features of the basic constructs underlying most biological-control programs. Their origin can be traced to the early 1900's, when ecology was beginning to emerge from its purely descriptive phase. They found their expression then in verbal and arithmetic arguments, but by the 1930's the essential ideas began to appear in the form of mathematical models. These models borrowed heavily from the tools, languages, and concepts of classical physics, and the models therefore took essentially the same form as classical physical models. Both the verbal and mathematical models were characterized by concentration on a very narrow array of components and by an essential simplicity of form. They often concentrated on equilibrium conditions, ignoring the transitional states that are an essential character of many pest outbreaks; even when they did not, temporal changes were handled in a very arbitrary and unrealistic manner. Spatial coordinates, too, were ignored, and populations were considered, for the sake of simplicity, as being evenly distributed over their environment. In short, the models were unidimensional.

The real world, however, is not unidimensional, and ecological systems are not characterized by a few components with simple actions and interactions. There is, first, an essential historical element in communities, populations, and individuals, since events at any moment depend on previous circumstances as well as on existing conditions. This was recognized in part by Nicholson in the 1930's, when he argued that models should include those temporal discontinuities caused by discrete generation times. His model, therefore, permits the computation of events within one generation, and the resulting output provides the initial conditions for the next generation. This represented a major advance and directed attention to the role of delays in causing instability. Discontinuities and lags are not, however, confined only to intergeneration breaks. There are short-term historical effects where, for example, a predator's rate of search is a reflection of the way its hunger level has been determined by its success in capturing prey in the previous hour, day, or even week. There are longer term effects where a predator's size and other attack parameters are determined by its nutritional history from birth and by that of its maternal parent, as well. There are still longer term historical effects imposed by seasonal changes and even more extended ones arising from long-term climatic fluctuations measured in terms of years. The effects of interactions between these various time-dependent changes, and the consequences of the inevitable historical effects that must result, are not known.

Second, realistic spatial effects have been eliminated from population theory even more completely than historical effects. Yet the appearance of pesticide residues in Antarctic penguins and of radioactive contaminants in the food of Arctic caribou bear witness to the interaction of events over large areas of the earth. If interactions can occur over such long distances, they can certainly occur within smaller areas dominated by separate communities. Even within such small areas, there is a mosaic of physical and biological properties, and the events in each element of the mosaic are linked to those in other elements by a variety of physical and biological transport systems. A sporadic upsurge of population in one element could therefore spread to other elements, or a population disappearing from one locality could be reinstated by immigrants from other localities. These perturbations are presumably damped by the way dispersal processes interact with spatial heterogeneity of the environment and temporal fluctuations of climate and organisms.

Remarkably little effort has been directed toward these problems, but the results of two recent studies hinted at their significance. One was a laboratory study of the interactions between a predatory and a phytophagous mite in artificial ecosystems. The resulting fluctuations in populations of predator and prey could only persist when sufficient dispersal barriers were introduced to produce a biological mosaic. Without barriers, the interaction was completely unstable. Some of the relevant mechanisms have been explored in the second study, which is a compelling and unique field and laboratory analysis of populations of the western tent caterpillar, *Malacosoma pluviale* (Dyar), in western Canada. The topographic variation in these areas produces a pronounced mosaic of habitable and unhabitable localities that change qualitatively and quantitatively as weather patterns change from year to year. Moreover, tent caterpillar individuals are not identical to one another but appear as qualitatively distinctive types with different vigor and dispersal properties. The vigorous individuals that disperse actively are the first to colonize a locality that has just become habitable. As the age of the local infestation increases, however, the proportion of vigorous individuals declines, since they tend to disperse away from the area. Hence, the densities and the kinds of tent caterpillars found in one spot are a consequence of the way dispersal mechanisms interact with environmental and biological changes in time and space. The relationships are extremely complex, but they should obviously be of direct and central concern to population biology. They have not been of such concern.

The visualization of population and community structure arising from classical population theory does not conform to the real world in a third and final way. Because of the large number of components in a community and the complexity of their actions and interactions, population biologists have been forced to simplify in some manner. Although simplification is always necessary to prevent constructs from becoming smothered in detail, it can, however, be carried to the point where the construct bears no meaningful relation to the events studied. In the days before the computer, the only solution to the problem of complexity was to assume that no more than two or three agents affected a population, that the individuals in the population were identical, and that their actions and interactions were of the simplest kind. Only by making these assumptions did it become possible to apply the mathematical languages and concepts that had proved so powerful in classical physics. Events in nature, however, occur in a fundamentally more complicated manner than that suggested by these assumptions. Not only are there many classes of population processes operating simultaneously—predation, parasitism, disease, dispersal, competition, and climate—but each one is represented by several agents, each of which can operate quite differently. These agents interact in a variety of ways, both within and between trophic levels, and the consequences of the magnitude and kinds of interactions are just beginning to be explored. The characteristics of each of these processes can be traced to the action and interaction of a number of components. In a recent experimental and mathematical study of predation, for example, the response of individual predators to prey density could be traced to ten components, of which no more than three have been considered in classical studies. The possible combinations of these ten components yield 32 structurally different kinds of predations, each of which has a different effect on prey populations. As a demonstration of the order of complexity of predation, the computer simulation model developed from these studies has over 800 separate statements. Classical predation models can be written on a single line. The real world therefore differs from the world conceived by classical population theory by several orders of magnitude, and, despite the pragmatic need to simplify, the degree of simplification forced on population biologists has a high probability of grossly distorting our conception of the role of biological-control agents.

The central cause of the incompleteness and unreality of population theory lies in the limitations of the mathematical language and approaches borrowed from classical physics. Early attempts to construct mathematical models of population events quickly encountered the problem that if the models were based on realistic assumptions, they became completely intractable mathematically. The model-builder therefore learned to develop models based on a small number of simple assumptions and to live with the fact that the models did not correspond too closely to the real world. By adopting this *modus vivendi*, however, all motivation to support theory with fact and establish an intimate feedback between theory and experiment disappeared. Yet it is such interaction that has historically generated the major advances in science. As a result, very early in the development of population biology, a dichotomy arose between biomathematicians and field and experimental biologists. Both groups have suffered from the separation.

COMPUTERS AND POPULATION BIOLOGY

The development of large digital computers at last promises to change this situation profoundly. The great computational speed of modern computers, their large memory capacity, and the availability of powerful programming languages are admirably suited to handle the specific features of ecological systems that make them so complex and apparently intractable.

The problem of including a spatial element, for example, can be solved by visualizing an area as being divided by a grid into discrete subsections. After the relevant events are simulated in each subsection, dispersal processes can be reproduced to determine how subsections affect one another. This reduces the spatial problem essentially to a bookkeeping chore—the very task delegated by so many businesses to digital computers. Such a model has already been developed in a very preliminary form, and it provides the way to determine the consequences of various strategies of biological control—of the merits, for example, of introducing small numbers of parasites in several localities as against a large number in one.

Similarly, the digital computer permits the ready incorporation of an historical element. Just as space can be divided into subsections, so time can be divided into elements, and events can be computed within the time elements consecutively. Thus, the great computational speed of the computer allows the biologist to simulate all the relevant history of the system he is studying. It becomes possible, for example, to simulate a perturbation of the system and to determine if there is a critical time before or after the perturbation when the introduction of a natural enemy would have the greatest stabilizing effect.

Finally, the same features that allow the inclusion of spatial and historical effects permit the biologist to include all the relevant components of most ecological processes or systems. Moreover, certain features of available programming languages are ideally suited to express realistically the particular kind of actions of and interactions between these components. Thus, the prevalence of thresholds, limits, discontinuities, and nonlinearities in ecological systems no longer presents the insoluble problem it did before the development of computers.

Although computers and their languages are remarkably well suited to cope with the magnitude and kind of complexity inherent in ecology, their great promise can, paradoxically, inhibit rather than enhance understanding. It is so easy, faced with a language of such power and facility, to forget that what is said in that language must be real and meaningful. When so many components operate, their modes of action and interaction are not intuitively obvious, so that the research program must be given detailed direction through an intimate wedding of computer-oriented techniques of synthesis with experimental methods of analysis.

ANALYTICAL PROCEDURES

The complexity of ecological systems presents as many unique problems of analysis as of synthesis. The variety of components and the complexity of their actions and interactions demand a special kind of analytical procedure that will unravel the complex maze of causal pathways in order to yield precise and biologically realistic constructs. In the process, the constructs cannot become so smothered by detail, so colored by the specific examples chosen for study, that they lose all generality. Biological control programs cannot flourish if we know only, for example, how specific predators operate. We must know how all predators act.

The joint need for reality and generality presents an extremely difficult problem of anlysis, since biological systems are remarkably diverse. Consider the variety of search and capture techniques that have been developed by predators. One predator will grasp prey, and another will filter out prey with a sieve; one will ambush, while another actively moves in its search for prey; one will eat all it kills, but another will eat only some of the prey killed and will hoard or discard the remainder; one will hunt alone, and another will hunt in a pack. This multitude of solutions to specific problems imposes a diversity that seems overwhelming, that seems to obviate any generality in a specific model. However, no matter what specific search or capture techniques are employed, every predator has to spend time pursuing, capturing, eating, and digesting prey, and, since time is limited, the way a predator portions its time determines how many prey it captures. Thus, underlying the diversity in nature is a unity, a universality imposed on all matter by the demands of space and time, and on broad taxonomic groups of animals by reason of their common organization.

As a result, certain components of any ecological process are found in all examples of that process and can be termed basic. The diversity occurring in nature is caused by the appearance of additional, subsidiary components, present in some situations but absent in others. It has recently been discovered, for example, that a predator's response to prey density arises from the action of five basic and five subsidiary components. Since the five subsidiary components can be present or absent, there are five possible dichotomies and 2^5, or 32, structurally different kinds of predation. In order to retain generality, therefore, it is only necessary to identify the basic and subsidiary components of a process and then devise methods to show how each component acts and interacts with others. A simple situation is first discovered that includes only the basic components. Preliminary experiments suggest groups of hypotheses to explain the action of each component, and these postulates are then tested by devising experiments that are critically designed to exclude one or more of the hypotheses. Although this approach is basically the old-fashioned method of inductive inference that goes back to Francis Bacon, it has two key features that have justified the recently proposed name of strong inference. It first emphasizes the need for the erection of multiple hypotheses, and, second, the need for experiments to show which ones are inadequate.

Once a set of postulates is proved adequate, it can be expressed in a mathematical form and the equations can be synthesized to produce a model of the basically simple example chosen. This provides a base from which to explore more complex examples, where additional, subsidiary components operate; these new components and their interactions can be analyzed in the same way, and the basic model can be expanded to include them. In this way, a more and more complex structure is built, each progressive step being taken only when a valid explanation has been obtained for previous steps.

This analytical procedure forces an organization on the analysis of complex systems by directing attention to small groups of components: first, to those that are universal properties of the process; second, to those that are shared by only some examples. The resulting model is gradually expanded, in many small steps, to include more and more of the process, and at each step there is a constant feedback between theory and experiment. As a result, the model is realistic and general, for any specific situation can be simulated by removing those subsidiary components that are absent in that situation. The great value of this experimental components analysis lies in the blending of two powerful methods of science; the comparative approach that has found its greatest expression in evolutionary theory, and the technique of strong inference that has provided such deep insights into problems in particle physics and molecular biology. Experimental components analysis provides the necessary kind and quantity of information to capitalize on the great promise of computer-oriented methods of synthesis, since the methods both of analysis and of synthesis are indivisible partners in the development of realistic and generalizable constructs of whole ecological processes.

OPERATIONAL PROCEDURES

Models of the kind described above promise a revolutionary change for biological control programs. At present, biological-control practices involving natural enemies of pests are based on relatively few operational guidelines. It is first of all presumed that predators, parasites, and diseases of pests are all candidates to introduce in an area where they are lacking. This conviction is supported by classical population theory, but its fundamental basis of support lies simply in the belief that an animal that kills a pest is "good." This is hardly sufficient as a prime basic premise in such a complex area of application. There is also a very real chance that it can be wrong. There has long been a controversy, for example, concerning the possible disadvantages of introducing as many species of parasites of a pest as possible. Some argue that this is the only way to assure the best possible combination of parasite species. Others feel that there might be a very real possibility that one or more of the introduced species would compete so effectively with parasites with efficient methods of search that the total controlling effect of all species would be reduced. No one really knows which position is correct, and the persistence of this controversy is a testament to the inadequacy of basic information in population biology.

A corollary to the premise that an animal that kills a pest is "good," is that one that kills the killer is "bad." As a result, parasites collected for introduction are carefully quarantined and reared to prevent the introduction of their hyperparasites. But a deeper insight into the action and interaction of populations of organisms might show that some kinds of hyperparasites can promote stability in pest populations. It was pointed out earlier, for example, that parasites can act as delayed negative feedback agents, and that such agents can produce instable oscillations in pest numbers. A hyperparasite could damp these oscillations by limiting the numbers of the primary parasite whenever it built up to the excessive numbers involved in the generation of wild oscillations. Until realistic, holistic, and generalizable models are constructed, there is no way to determine exactly how the relevant components of attack interact over time and space. Basic concepts are so incomplete that we cannot afford to exploit the potential advantages of hyperparasites now, because of the possible disastrous consequences.

There are many other operational guidelines, expressed as generalities, concerning the efficiency of natural enemies. It is presumed, for example, that predators and parasites should have a high searching capacity to enable them to find prey and hosts when they are scarce; that short developmental times and high fecundity of parasites are important but secondary; that specific predators might be more consistently effective than ones with generalized feeding habits; that superparasitism should be minimal. In every instance, however, these generalities can be traced to incomplete or unrealistic basic constructs or to the results of isolated empirical studies. In each case, an argument can be devised, as previously discussed, involving spatial and temporal effects and interactions with other population processes that makes them suspect.

Existing operational guidelines are incomplete and inadequate, because the basic constructs of population biology do not conform to the real world. When models are constructed by wedding insightful analytical procedures with the great power of modern computers, it will be possible to use the models to simulate the real world and thereby erect precise operational procedures. The most important attributes of a natural enemy in population regulation, for example, can be determined by assigning a range of values to each attack parameter and by simulating the consequences of each value. It will be possible to perform experiments with the models that would be impossible to perform in nature because of expense, time limitations, or possible disastrous consequences. The action of hyperparasites, for example, can be simulated in order to demonstrate the possible effects on population stability, and parasite releases can be simulated with different timing and spatial distribution to show the resultant effects. Once temporal and spatial elements are realistically incorporated in simulation models, it should become possible to discover new methods of biological control involving manipulation of periods of oscillation of pest numbers. That is, it might be possible to reduce the amplitude of oscillations, not by killing pests, but by changing the period of oscillation, and thereby remove the instabilities that arise from the interaction of historical processes. In this view, therefore, attention is switched from those attributes of a natural enemy directly determining the number of pests killed to those attributes affecting the historical development and spatial distribution of populations. Thus, the length of the development of a parasite becomes of more central concern than rate of attack. Superparasitism and hyperparasitism become potential benefits because of their properties of damping oscillations. A control procedure might even be suggested by the simulation studies that would actually increase pest density briefly in order to switch populations into more stable oscillations. In short, a new world of operational procedures can emerge, now that techniques of analysis and synthesis have become sophisticated enough to yield basic constructs that conform to nature.

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CHAPTER 8

Microbial Control of Insects

Microbial control may be defined as the use of microorganisms by man to control other species; in entomology, microbial control is one of the techniques employed in the biological control of insects.

Disease symptoms in insects, particularly in beneficial insects such as the honey bee, *Apis mellifera* Linnaeus, and the silkworm, *Bombyx mori* (Linnaeus), were noted as early as 2700 BC in China, and later in ancient Greek times. The first truly scientific approach to the study of an insect disease was the investigation of the white muscardine disease of silkworms (known in Italy as "calcino"), caused by the fungus *Beauveria bassiana* (Bals.) Vuillen. The classical work by Pasteur in France, on the "pebrine" disease of the silkworm, caused by the microsporidian *Nosema bombycis* Nageli is famous and is cited in most microbiological textbooks. The idea of using the microbial agents for insect control was first recorded in the eighteenth century; mass production of *Metarrhizium anisopliae* (Metch.) Sor. was carried out in an attempt to control the sugarbeet curculio, *Cleonus punctiventus* Germ.

Despite the early beginnings made in the study of infectious diseases in insects, the field of insect pathology and microbial control has until recently lagged far behind human and veterinary medicine. Perhaps an explanation for this is in the rather unfortunate choice of organisms used in early attempts to kill insects. In Europe, several workers tried to use fungi to control insect species in the late 1800's. At about the same time, the fungus *Beauveria globulifera* (Speg.) was used in the United States in an attempt to control the chinch bug, *Blissus leucopterus* (Say). Most of these early efforts ended in partial or complete failure, because of the inability of the investigator to control the environment and his lack of knowledge of the fungus populations he was using as control agents.

With the knowledge of hindsight, it is tantalizing to speculate what would have developed in the field of microbial control if the fine scientists in the past had used some of the nuclear polyhedroses viruses of Lepidoptera, or such bacteria as *Bacillus popillae* Dutky, the causative agent of milky disease, or *Bacillus thuringiensis* var. *thuringiensis* Berliner, a pathogen of Lepidoptera and Diptera.

Starting in the late 1920's, earnest efforts were made in Canada, France, and Hungary to control the European corn borer, *Ostrinia nubilalis* (Hübner) by using microbial agents. This work was encouraging, but was not carried very far. A recent, more basic approach to the study of insect diseases is providing the key to the solution of many of the frustrations that plagued early investigators in their attempts to use insect pathogens. Such basic studies require laboratories equipped and staffed to study all phases of microbial control.

PATHOLOGY OF INSECTS

Fortunately, most of the microorganisms capable of causing disease in insects do not harm other animals or plants, and, conversely, man's pathogens generally do not cause disease in insects. This is one of the most important factors encouraging the use of insect pathogens as control agents.

New organisms are being isolated and described each month. Already, 1,165 microorganisms have been found associated with insects; most of these are pathogens. This total includes 90 species and varieties of bacteria, 260 species of viruses and rickettsiae, 460 species of fungi, 255 species of protozoa, and 100 species of nematodes.

It was quite natural that microbiologists studying infectious diseases in insects should draw heavily on the wealth of experience developed in medical research. They at first accepted the idea that a suspected microbial agent must satisfy all the following conditions of Koch's postulates before it was considered an insect pathogen: (1) the microbe must be identified microscopically and isolated in all cases of diseased insects having the same symptoms; (2) the suspected organism should be grown in pure culture, on artificial media; (3) the pure culture of the organism must be reintroduced into healthy specimens of the host species and must cause similar symptoms to those first recorded; and (4) the suspected organism must be isolated from each case of the disease with the specific symptoms. These requirements were suitable for establishing the pathogenicity of fungi and bacteria that grow readily on artificial media; however, when fastidious bacteria, protozoa, rickettsiae, and viruses were discovered in insects, the criteria had to be modified.

Accordingly, when dealing with an organism that cannot be cultured on artificial media, the following two steps must be taken to establish its ability to cause a specific disease.

1. The microbe must be identified and isolated from all cases of diseased insects having similar symptoms; if necessary, the identification may involve use of the electron microscope. These criteria apply mainly to protozoan, rickettsial, and viral infections, although they may be applied to all fastidious pathogens. An immediate and thorough histopathological examination of all tissues is imperative. The electron-microscopy phase may be quite extensive, involving thin sectioning of diseased tissue and of the polyhedra of viruses; chemical dissolution of the polyhedra to investigate the type, size, and distribution of virus particles; and, possibly, making carbon replicas of polyhedra to determine the external shape.
2. Healthy specimens of the specific host must be infected with the isolated microorganism, and the microbial agent must be reisolated. The isolation of these organisms may require extensive application of the most modern techniques to obtain the suspected organism in pure culture. This may involve ultracentrifugation, gel and agar column diffusion, electrophoresis, or sugar gradient techniques.

Collection of sufficient microbial agent to reproduce the disease so that it is available to other interested scientists should be carried out, because several pathogens are so rare that their existence, once isolated, depends on this practice.

The problems of diagnosis and isolation of a pathogen may be complicated by several phenomena with particular reference to bacteria and fungi.

1. Two grossly similar yet significantly different disease organisms may habitually coinfect a given host. For example, recent investigations have shown that two polyhedroses diseases are consistently present in viral populations of the cabbage looper, *Trichoplusia ni* (Hübner), collected in the United States. Scientists had previously presumed they were dealing with a single disease in this insect species.
2. The true pathogen may be cast out of the body at the point of death, such as the evacuation of spores of *Clostridium brevifaciens* Bucher from the gut of larvae of the western tent caterpillar, *Malacosoma pluviale* (Dyar). In such a case, the secondary invaders are often suspected.
3. Similar disease symptoms can be caused by several microorganisms acting separately, as in the case of European foulbrood.

4. A group of insects may die from physiological causes, and secondary invaders or normal gut flora may be suspected. In insect rearings, this complication is often seen.

5. Insects may have sublethal infections, such as those caused by low but constant doses of toxic crystal-forming bacteria, or they may have low-level unapparent infections (often, and perhaps improperly, called latent infections).

6. A disease may be caused by two organisms acting in concert, such as the DD 136 nematode and its associated bacterium.

ROUTES OF INVASION

Generally speaking, there are four means of infection:

1. Oral infection, whereby an organism is ingested with food. Viruses, rickettsiae, bacteria, nematodes, protozoa, and possibly some fungi all gain entrance to the insect's body by this route.
2. Invasion through the intact integument or trachea is the most common route used by fungi and by some nematodes.
3. Parenteral invasion. Most microorganisms can invade when trauma to the integument occurs, usually as the result of biting or wounding by an ovipositing insect parasite.
4. Transovum passage of microorganisms such as viruses, rickettsiae, spirochaetes, and protozoa, either in or on the egg, is quite common.

THE INFECTION PROCESS

The outstanding fact to emerge from the last two decades of intensive investigations on microbial control is the importance of basic and intimate details of the infection process in the case of each disease. Only through the possession of such details can microorganisms be produced with knowledge and used confidently against insects in the field.

There is a subtle but important difference among the terms virulence, infectivity, and pathogenicity. Since these words are often used indiscriminately in the literature, it might be appropriate to define their meaning as used in the following presentation. Virulence, or virulency, is the relative capacity of a microorganism to overcome the body defenses of the host. Infectivity is the ability to produce infection—the tendency to spread rapidly from host to host. Pathogenicity is the capacity to cause disease (morbid reaction of the host) and is a fixed inherited quality of a microorganism in relation to each potential host considered. In discussing the infection process, it is essential that there be a thorough understanding of the interrelations between these parameters. In insect pathology, virulence must be considered as two distinct capacities: the ability to invade the host and the ability to multiply and kill the host. Selection for virulence in strains of fastidious microorganisms growing only in the insect, and having resistant forms that remain viable in the environment to infect new hosts, is a precise and important operation. A strain of *Bacillus popilliae* was chosen because it invaded very rapidly in the first phase but was of medium virulence in the second phase. The host remains alive for days with the result that bacterial multiplication, and the number of spores produced per insect, increase. Since the degree of virulence in the second phase governs the number of infective units released into the environment, it also influences the infectivity. This principle applies to the fastidious protozoa, viruses, nematodes, and bacteria that have resting stages that remain infective in the environment for considerable lengths of time.

CHANGE IN VIRULENCE

Apparently, bacteria and fungi are much more susceptible to change in virulence than are viruses, rickettsiae, and protozoa. The variability of the latter types of organisms might in many cases by masked by changes in the host, since these fastidious organisms are entirely restricted to the living host cell. Insects are so variable that the changes in the host may be of greater significance than changes in the fastidious pathogen. Increases in the virulence of insect pathogens have been detected after (1) passing the organisms through susceptible animals; (2) mixing pathogenic species before introduction into the host; (3) mixing pathogens with substances, e.g., starch and mucin, that protect the organisms against damage by gut contents and defensive materials, or mixing them with agents that aid invasion, such as ground glass; and (4) selection of virulent strains from a less virulent population by various techniques after causing dissociation.

However, microorganisms may suffer loss of virulence by (1) stressed dissociation to low and highly virulent forms, (2) cultural conditions that are abnormal, (3) passage through unsuitable hosts, and (4) culturing at abnormally low or high temperatures.

Populations of microorganisms that cause death of insects differ in various parts of the world, and large differences in virulence have been detected between geographically isolated strains. However, much remains to be discovered concerning this variability of insect pathogens.

CELLULAR IMMUNITY

It is of historical interest that the ability of free blood cells to engulf invading organisms was first discovered by Metchnikoff, who used the water flea, *Daphnia* sp., an arthropod, as a test animal. He termed this process phagocytosis.

For years, insect pathologists thought that phagocytosis was the main response to invasion of the blood by organisms. Early students of this process in insects established that fungal and bacterial invaders in the insect hemocoel were destroyed by the blood cells in a variety of ways: (1) by phagocytosis and destruction of the bacteria by intracellular digestion, (2) by the formation of capsules, a product of blood cells, (3) by the formation of giant cells made up of cell masses, and (4) by the formation of abscesses. Now we know that most insect blood cells carry out a phagocytic function to some degree. The hemocytes generally respond to most foreign materials introduced into the body cavity.

Recent studies suggest that the blood cells in insects are attracted to living or inanimate objects in the hemolymph that do not have a specific coating that covers all tissues in the specific insect. Foreign particles in the blood stream are invested by a mass of blood cells depositing what appears to be a mucopolysaccharide coating on the object; living objects are simultaneously coated with melanin. This coating usually kills the foreign organism, thus preventing proliferation or growth. Apparently, after the coating is deposited, most of the surrounding phagocytes disperse in the hemocoel. It is postulated that phagocytes detect tissue that is not coated with the specific mucopolysaccharide covering.

Although phagocytosis is often an active system of immunity in insects, much more intensive work is required before the relative protective value of the system is established. Many species of bacteria kill insects very rapidly when injected in fairly small numbers into the hemocoel. Although phagocytosis takes place on many of these occasions, it is rarely successful in protecting the insect. Other invading organisms produce toxic materials that can destroy phagocytes. However, there are many microorganisms that are harmless to the insect even when massive doses are injected. Since the insect hemolymph provides a good medium for saprophytic organisms, there must be some explanation for the failure of such organisms to grow. Phagocytosis is certainly one of the deterrents.

HUMORAL IMMUNITY

There have been many reports of the detection in insects of antibodies comparable with those found in vertebrates; however, most of these reports have been disproved. Vertebrate antibodies are named according to their specific action, i.e., agglutinins, precipitins, complement-fixing antibodies, opsonins, antitoxins, and bacteriolysins. Although nonspecific materials such as interferon and properdin have been isolated from vertebrates, they have not been demonstrated in insects; nevertheless, nonspecific antibacterial agents, mainly of a bactericidal nature, including bacteriolysins, have been found in insects. Other antibodies listed above have not been demonstrated, and the consensus is that insects do not produce them. In vertebrates, these humoral defensive mechanisms make it virtually impossible to transfer tissue from one individual of a species to another. The fact that tissue transplants can readily be made in insects supports the conclusion that insects have no antibodies comparable with those in vertebrates.

There is evidence of the presence of a small molecule in insect blood that has a lytic effect on bacteria, and this action may be connected with the process of melanization in insect blood. Silkworm larval blood melanizes in cold storage and loses its antibacterial properties proportionally, and blood from larvae of the greater wax moth, *Galleria mellonella* (Linnaeus), that have been immunized against *Pseudomonas* sp. does not melanize on exposure to air. Some possible explanations of these and other similar observations should be investigated: (1) the process of melanin formation ties up phenolic compounds that are normally free in the blood, and phenols are nonspecific germicides; (2) proteins are bound to melanin and are removed from solution during the process of melanization. According to one investigator, the presence of a small, bactericidal molecule associated with proteins that might be removed from solution during this process has been postulated. Much remains to be investigated in this area.

Actively Acquired Immunity

Attempts have been made to immunize insects with most of the antigens effective in mammals, including toxoids, vaccines made from attenuated living organisms, organisms killed with heat or chemicals, and various extracts from microbial pathogens. The results of most of these experiments are questionable, except when vaccines were employed. The consensus is that insects build up a nonspecific immunity to some bacteria after a course of injections of vaccines prepared from the bacterial culture. This immunity is short-lived, rarely lasting more than 3 to 4 days, the period depending on the technique used. It has been impossible to induce immunity in insects through the oral administration of vaccines. Much remains to be done in developing techniques peculiar to the study of immunity in insects. This may involve shedding some of the ideas from vertebrate immunological studies.

Passively Acquired Immunity

Mammals and other vertebrates may be protected by transferring blood from a previously immunized individual. Very little work has been done with insects in this area. However, it is possible to transfer blood from previously vaccinated individual insects and obtain a short-lived protection in the recipient of the transfer.

EPIZOOTIOLOGY

Insect populations are dynamic entities, constantly fluctuating in adjustment to a host of parameters, many of which are probably unknown. Climatic changes, pathogens, parasites, predators, and availability of food are a few of the factors involved. The populations may be composed of several types of individuals with regard to disease. These types are (1) the typically diseased insect, (2) the atypically diseased insect, (3) the latently infected insect, (4) the healthy carrier, (5) the uninfected susceptible insect, and (6) the uninfected immune insect.

Not all the above types are necessarily present in all populations in the presence of all known kinds of infectious agents. Furthermore, there has not been adequate proof of the existence of occult pathogens in insects; they may or may not exist. Consequently, the latently infected insect and the healthy carrier should be considered as the same type until proof of latency is presented. Since insects do not produce recognizable antibodies, the task of establishing the presence of an occult virus is extremely difficult and requires the same type of rigorous protocol and techniques used in virus laboratories studying the most infectious human pathogens.

RESISTANCE TO DISEASE

Resistance to disease is directly connected to the physiology of the insect. There are many clear-cut examples of such resistance in insects, but only a few can be explained.

Resistance to infection or to toxic by-products of insect disease organisms varies with the developmental stage of the insect when attacked. Early-instar larvae are usually more susceptible to virus infections than are last-instar larvae. This phenomenon is found in silkworm larvae fed toxic crystals of *Bacillus thuringiensis*. The prepupal stage of some sawfly species is resistant to infection by gut nuclear polyhedrosis virus, whereas larvae, pupae, and adults are susceptible; this is attributed to the change to resistant embryonic cells in the prepupal gut.

The adult insect is rarely affected by bacteria and viruses lethal to the larva, but it may be infected by these organisms and transmit them to the offspring. However, protozoa, nematodes, rickettsiae, and fungi may attack adults and larvae with impartiality, causing death or a reduction of fecundity in the adult insect.

Because of the composition and structure of the exoskeleton, pupae of some insects are resistant to some of the pathogenic fungi. The insect exoskeleton is a protein–chitin (*N*-acetyl glucosamine) mixture laid down by the secretions of the hypodermal cells. The secretion is hardened by a process of sclerotization of the protein and is coated with a waxy epicuticle containing unsaturated fatty acids and substances, such as 3-4 dihydroxybenzoic acid, that inhibit fungi. The insect may slough off incipient invasion by fungi when it molts.

Resistance of many larvae to infection by bacteria can be explained by conditions in the gut of the larvae. The high reducing conditions and the high pH (9.0 to 10.5) in the gut of some Lepidoptera apparently discourage growth of bacteria. Other lepidopterous larvae have a relatively low alkaline reaction in the gut (pH 7.0 to 9.0), and, other factors excluded, such insects are more susceptible to infection by bacteria. Phytophagous Hymenoptera also have a relatively low pH of the midgut, ranging from 6.5 to 9.0, and, significantly, they often are also more susceptible to bacterial infection. Orthoptera, however, usually have an acid reaction in the midgut, which is apparently inhibitory to bacterial growth, although some bacteria can apparently survive in the gut for considerable periods of time. Hard-shelled insects, such as grasshoppers, that lead an active existence, frequently tear the gut and cause death through a septicemia.

Many phytophagous insects feed on plants containing bacteriostatic and fungistatic substances, thus protecting themselves from potentially dangerous invaders. The importance of this in microbial control of insects by the use of bacteria has been underestimated. The larch sawfly, *Pristiphora erichsonii* (Hartig), is susceptible to certain strains of *Bacillus cereus* Fr. and Fr., when feeding on summer foliage. However, the larch tree, *Larix laricina* (DuRoi) Koch, collects an antibacterial substance in the leaves during August and September that completely inhibits the bacterium and infection in this insect.

There have been several reports of increased resistance to virus diseases in Lepidoptera. These records were given as examples of acquired resistance in insect populations. Actually, they seem to represent selection of resistant individuals from an insect population under continual pressure by an infectious agent. The potential to resist was innate and was probably not acquired. In most virus cases studied, the possibility of the virus changing in virulence or infectiousness was not investigated. This does not exclude the possibility of mutations occurring that might block the process of invasion of a given pathogen, although no such case has been described. The ability of the honey bee to open and clean out cells containing larvae infected with *Bacillus larvae* White (American foulbrood) depends on two genes that control housecleaning habits. Bees with both genes are more resistant to American foulbrood than are bees with only one gene.

In the field, the incidence of bacterial infection of insects drops decidedly at temperatures below 20°C; increases in temperature up to 37°C increase the incidence of many forms of disease. However, some insects have become more resistant to specific virus diseases as the temperatures increased from 29.4 to 46°C. This is apparently an effect of the temperature on the invasion and multiplication of the virus in the insect.

In many insect populations, a break in the chain of events leading to infection has the appearance of resistance to disease. It is therefore extremely important to determine the details of the infection process and the fate of the pathogen in the field.

ENVIRONMENTAL CONDITIONS

Many factors influence the survival and growth of insect pathogens in the field and thus affect their infectiousness.

Temperature effects on invading organisms are varied and perhaps not properly understood. The incidence of infection by bacteria and fungi may be affected below 18°C, although some bacteria, viruses, and protozoa apparently infect more insects in the cool fall than in the hot summer. Warm weather generally increases the incidence of disease caused by fungi, bacteria, protozoa, and viruses. At times, high humidity and associated temperatures ranging from 15.6 to 21°C are necessary for decisive invasion and kill by some entomogenous fungi; these particular conditions also enhance the ability of some nematodes to survive and invade hosts.

The fall webworm, *Hyphantria cunea* (Drury), the armyworm, *Pseudaletia unipuncta* (Haworth), and the gypsy moth, *Porthetria dispar* (Linnaeus), succumb most readily to their respective viruses when the weather is warm and the humidity is very high. Whether high humidity affects the host or the development of the pathogen is not clear. However, many viruses do not develop rapidly unless temperatures of 21 to 29.4°C and relative humidities of 50 to 60% are experienced.

Sunlight (ultraviolet) has killed most insect pathogens against which it was properly tested; *Bacillus popilliae* spores, and vegetative cells and spores of *B. thuringiensis*, are destroyed on exposure to sunlight, and non-spore-forming bacteria perish rapidly from drying and on exposure to ultraviolet radiation.

The condition and reaction of soil may strongly affect pathogens. Fungi capable of attacking insects survive longer in soils with a high organic content. *Metarrhizium anisopliae*, *Beauvaria bassiana*, and other entomogenous fungi kill more frequently and persist longer in rich soils; however, because of the organic matter in them, such soils retain water longer than sandy soils or even sandy loams. Milky disease of the grub *Melolontha melolontha* (L.) appears to be more prevalent in rich soil than in soils of low organic composition. An acid reaction of the soil is unfavorable for spores of *Bacillus popilliae.*

Although there has been no extensive investigation of the interrelations between natural soil microbiota and insect pathogens introduced from dying insects, it is almost certain that antibiotics and metabolites produced by soil-inhabiting fungi and bacteria would have the same adverse effects on bacterial pathogens and entomogenous fungi in the soil as have been demonstrated in the test tube.

METHODS OF TRANSMISSION

When phytophagous insect larvae die of an infectious disease, their bodies disintegrate on the plant or on the ground, and the organisms contained in the cadavers are dispersed by wind, rain, or dew to other host plants or locations. Microorganisms in the gut of infected insects are distributed in the feces, and larvae infected by pathogens can be eaten by birds, wasps, or other predators, which spread the organisms in their droppings.

MICROBIOLOGY

VIRUSES

Taxonomy

The nomenclature of insect viruses is still under investigation by the International Nomenclature Committee. Recently, authorities have been most cautious in their evaluation of the status of viral taxonomy, and it is obvious that many changes will be made before a useful and proper system is available. However, some progress has been made during the last two decades, and the viruses pathogenic for insects will be included in the class Arthropodophaga and order Arthropodophagales.

There is a natural grouping of insect viruses based on (1) the presence or absence of a protective coating around the virus particles known as an inclusion body, (2) the morphology of this inclusion body, and (3) the area in the host cell where the virus develops.

There are seven possible genera (see Table 3); the first four have been accepted by the International Nomenclature Committee.

TABLE 3 Characteristics of Insect Viruses and Their Host Ranges

Genus	Virus Shape and Size	Polyhedra or Inclusion Body	Main Component Nucleic Acid	Insect Order(s) Affected	Tissues Infected
Borrelinavirus[a] (Paillot) Nuclear viruses	Rods 20–50 mμ by 200–400 mμ	Present 0.5–15 mμ	DNA	Lepidoptera Diptera Neuroptera	Fat body, gut, tracheal matrix, hypodermis, blood cells
Smithiavirus[a] (Bergold) Cytoplasmic polyhedra viruses	Circular 30–65 mμ diam	Present 0.5–25 mμ	RNA	Lepidoptera	Gut
Bergoldiavirus[a] (Steinhaus) Granule virus (Capsule virus)	Rods 40 by 400 mμ	Present 120–300 mμ by 300–500 mμ	DNA	Lepidoptera	Fat body (cytoplasmic)
Moratorvirus[a]	Circular 25–65 mμ diam	None	DNA or RNA	Lepidoptera Hymenoptera Diptera Coleoptera [b]	
Birdiavirus Nuclear polyhedra virus	May be identical to *Borrelinavirus*			Lepidoptera Hymenoptera	
Xerosiavirus	Virtually unknown—virus characterized by crescent-shaped polyhedra				
Steinhausiavirus	Granule virus—resembles *Bergoldiavirus* and found in nucleus				
Paillotellavirus	May be identical to *Xerosiavirus*				

[a] Accepted by International Nomenclature Committee.
[b] Also affects Arachnida.

Several new types of viruslike organisms have recently been isolated from insects. The nomenclatural structure proposed for the viruses pathogenic for insects will need enlargements and continual revision as our knowledge grows. It is essential that this be done with skill and caution, yet with alacrity, since the investigator must have precise knowledge of the identification of the organisms with which he works. The rule should always be to identify before more extensive work is attempted. Representatives of the various virus genera are pictured in Figures 12–17.

During the last 10 years, an intensification of interest in serology of insect viruses has given promise of a very useful tool in taxonomy, with obvious applications in diagnosis and epizootiology. However, serology can only be accurately used in taxonomy after surveys of the available organisms expected in any one host are completed. In some cases this has been accomplished, to the limits of our knowledge, but our knowledge is incomplete. No claim, for example, is made that nuclear and cytoplasmic granulosis viruses are the same or different species in any given host. Serological studies carried out with granulosis viruses have not shown whether or not the antigen is a mixture of two viruses; other analogous difficulties exist. Potentially, the serological identification of viruses promises to be of great use, but it is ob-

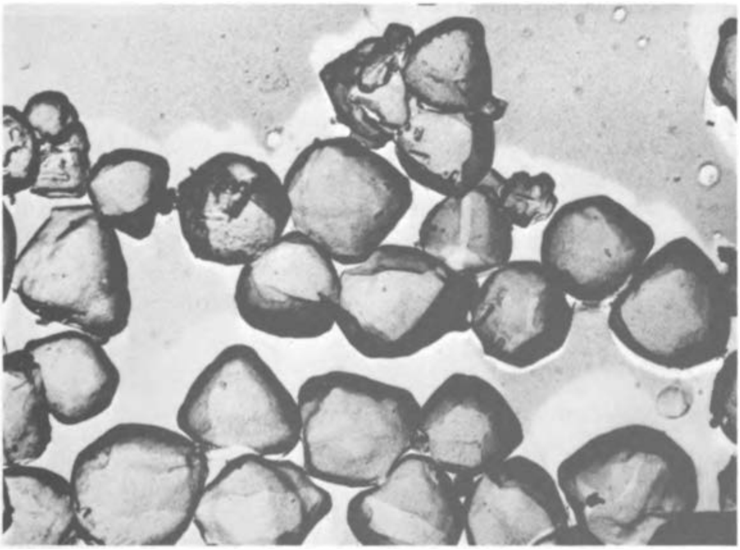

FIGURE 12 Carbon replica of the polyhedra of two nuclear polyhedrosis viruses coinfecting the cabbage looper, *Trichoplusia ni* (Hübner) (x 14,000). The polyhedra are identical in appearance. (Courtesy of the U.S. Department of Agriculture)

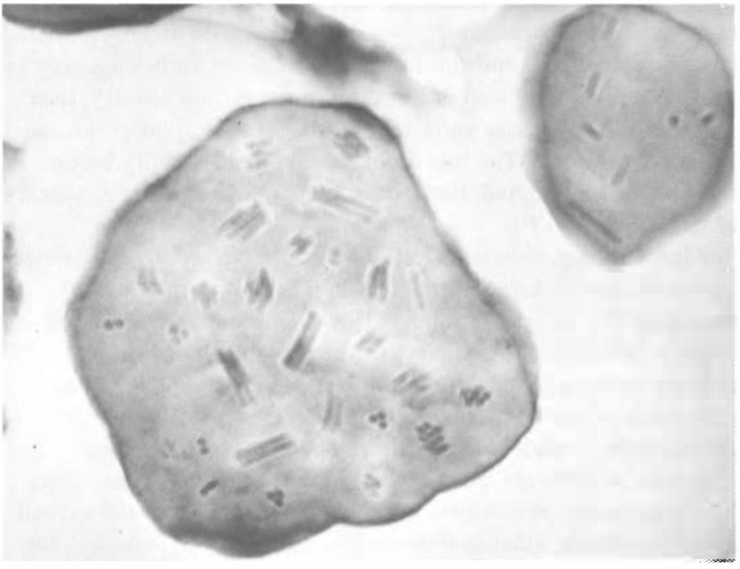

FIGURE 13 Sections of the two types of nuclear polyhedrosis viruses coinfecting *Trichoplusia ni (*Hübner), showing the packets of virus rods in one polyhedron and the single rods in the other (x 37,000). (Courtesy of the U.S. Department of Agriculture)

viously a tool that can be used accurately only by well-trained personnel in superbly equipped laboratories. For general use, it would be propitious to set up a world bank of sera, issued from such a specialized laboratory, to ensure that the ensuing studies are based on reliable working materials. International organizations interested in biological control could exert most welcome influences here. Sophisticated studies such as base-pair analysis of nucleic acids and DNA–RNA–residue phosphorous analyses of the viruses remain to be done in most cases.

Mode of Action

Information on the invasion of insects by viruses is limited, and theories are varied. Some workers have attributed an important role to the pH. This postulation is an interpolation of Bergold's method of dissolving polyhedra in sodium carbonate *in vitro*. Polyhedra of the nuclear polyhedrosis of the European spruce sawfly, *Diprion hercyniae* (Hartig), require much the same sodium carbonate treatment *in vitro* as do the nuclear polyhedra of the silkworm, yet the sawfly last-instar larval midgut pH has a range of 6.8 to 8.9, and the silkworm last-instar gut pH ranges from 9.3 to 10.4.

One author states that the protein from silkworm nuclear polyhedra protein (purified) contains 15% N and has 0 to about 0.06% P. Other workers estimate that the phosphorus content of whole polyhedra varies from 0.19 to 0.35% P, of which 50 to 60% is dialyzable phosphate produced during alkaline liberation of virus particles. One investigator isolated 5.8 to 7.8 mg/100 mg of RNA from purified polyhedral material. Most RNA run from 9 to 10% P; consequently, if one calculates the phosphorus content from the purified polyhedral material to be RNA at 6.8 mg/100 mg of polyhedra at 9% phosphorus, the resulting figure is 0.6% phosphorus. Obviously, there are some glaring discrepancies in the various estimates of phosphorus in the polyhedral material. A possible explanation of these discrepancies lies in the fact that certain phosphorus analyses are susceptible to interference by certain ions, such as silicon and arsenic.

A method was recently developed for estimating silicon content of polyhedra. With this technique, it was established that polyhedra of the nuclear polyhedrosis of *Heliothis zea* (Boddie) contain 0.12% silicon. The presence of silicon might explain the inert characteristics of the polyhedron. This subject is intimately concerned with the invasion of insects by viruses and also has a direct bearing on the storage qualities of polyhedra; therefore, it is worthy of further study. When the insect ingests the polyhedra, the release of the

FIGURE 14 Carbon replica of polyhedra from a cytoplasmic polyhedrosis of the pink bollworm, *Pectinophora gossypiella* (Saunders), showing pits left by escaped circular virus particles (x 13,000). (Courtesy of the U.S. Department of Agriculture)

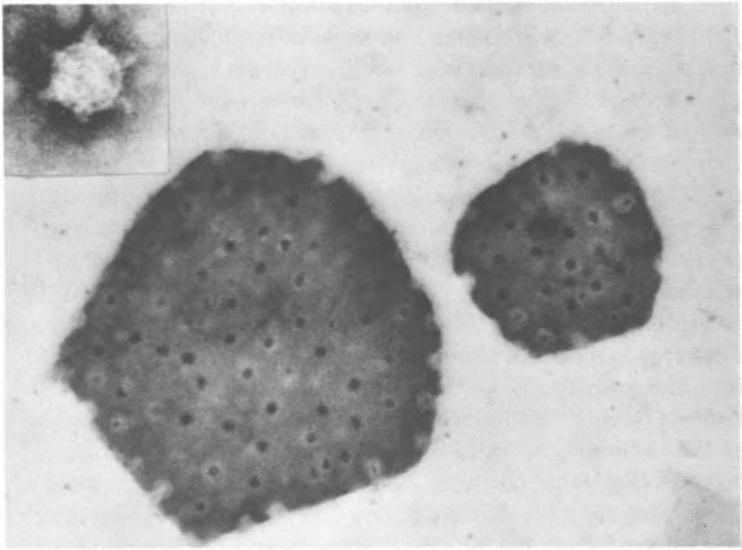

FIGURE 15 Sections of polyhedra from a cytoplasmic polyhedrosis of *Pectinophora gossypiella* (Saunders), showing circular virus particles (x 38,000). *Inset:* A single virus particle from the same disease showing characteristic projections (x 188,000). (Courtesy of the U.S. Department of Agriculture).

polyhedral protein does not involve proteolysis by enzymes, since the gut proteinases of several species of insects do not attack polyhedra.

The accepted procedure for dissolution of polyhedral protein consists of treatment of polyhedra with dilute sodium carbonate (0.004 to 0.03 *M*) in the presence of 0.005 *M* of sodium chloride at room temperature. Such a treatment is not capable of effecting proteolysis; however, it approximates the conditions existing in the lumen of the insect gut. If we bear in mind the efficacy of alkaline chloride solutions in the solubilization of silicates, and the fact that silicon is made soluble by carbonate–chloride solutions along with the polyhedral protein, the possibility that the release of protein depends on solution of silicon becomes plausible.

A secondary action by gut proteinases certainly takes place on the dissolved polyhedral protein, once released. This action may have a direct bearing on the invasive abilities of viruses. From LD_{50} studies, we know that virus species vary in their ability to kill insects, and one of the reasons for this variability can be explained by their capacity to survive in the gut. Apparently, naked virus rods do not survive indefinitely in the gut. The approximate period of survival, the time required for the infectious virus unit to invade the gut cell, and the identity of the invasive unit are not known. There is a so-called "eclipse phase," when the virus disappears in the body of the insect, that could be significant. The virus remaining in the gut contents is destroyed. Visually, the virus disappears within the cells; therefore, the invasive unit must be very small, and it may be much smaller than the virus particle. The virus antigen disappears, and serological detection is not possible; this probably means that the virus membrane is destroyed, since components of the virus membrane are undoubtedly the antigens we have employed in making sera. Since DNA is not antigenic, this leads us, by the process of elimination, to the hypothesis that the DNA strand, or a fraction of the DNA molecule that carries a compatible and complete message of coded base-pairs, must be the invasive unit.

The virus unit must enter and pass through the gut cell (or is phagocytosed) and passes through the basement membrane into the blood. There is no available information on the effect of the blood on the virus unit; this should be obtained. Finally, the virus unit enters the membrane of a susceptible cell (or is phagocytosed), passes through the cytoplasm, and enters the

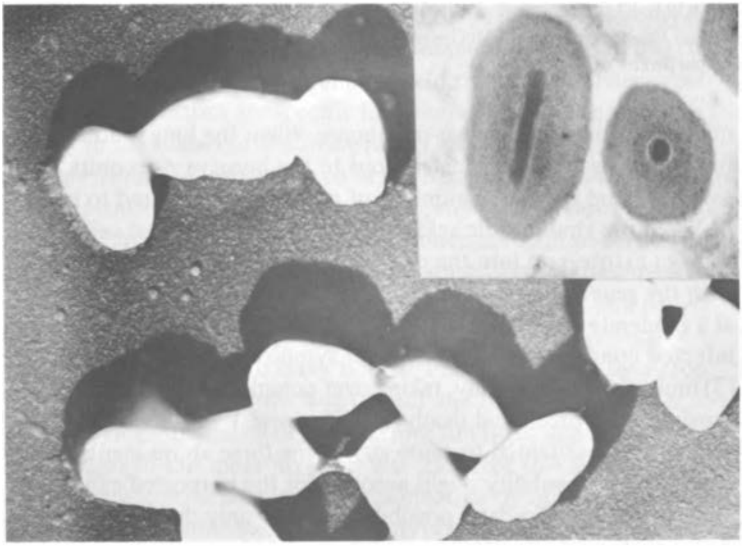

FIGURE 16 Granules from a granulosis of the salt-marsh caterpillar, *Estigmene acrea* Drury (x 45,000). *Inset:* A section of granules from a granulosis of the red-banded leaf roller, *Argyrotaenia velutinana* (Walker), showing the virus rod in longitudinal section (left) and in cross section (right) (x 66,000). (Courtesy of the U.S. Department of Agriculture)

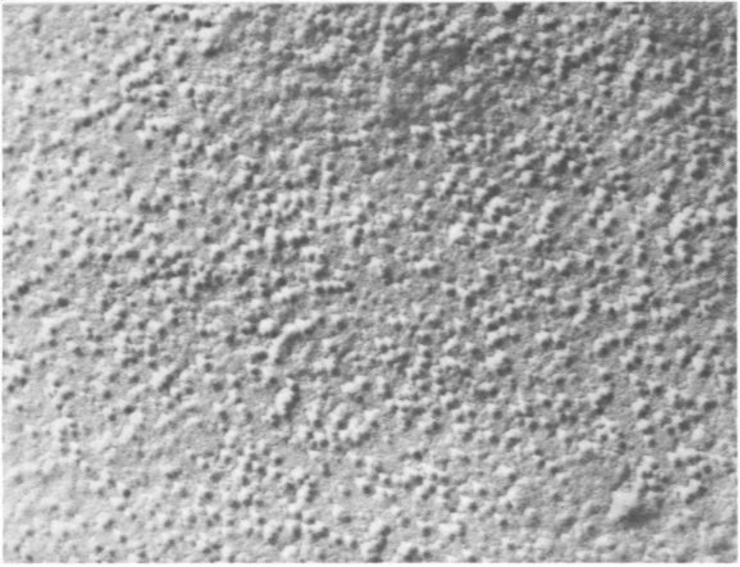

FIGURE 17 Circular, noninclusion virus from diseased citrus red mites, *Panonychus citri* (McGregor) (× 38,000). (Courtesy of the U.S. Department of Agriculture)

nucleus through the nuclear membrane. When the long journey is described fully, and if each stage is deleterious to the invasive virus units, one can begin to understand why large numbers of particles are required to infect the host.

When the viral nucleic acid enters the susceptible host cell during infection it may (1) integrate into the cell's genetic material, multiplying simultaneously with the genetic material of the host (not yet proved); (2) multiply in the cell at a moderate rate to preserve the integrity of the host cell or cause a chronic infected condition without external symptoms (not yet demonstrated); (3) multiply rather rapidly, taking over complete genetic control of the cell and causing acute virosis and death (typical viroses); or (4) remain static in the cell, with full potential to cause any of the three above-mentioned phenomena. The last possibility might account for the purported existence of so-called "occult" viruses. To date, possibility 3 is the only duly recorded process of the virus diseases in insects.

Many studies must be made before any other possibilities of infection can be accepted. This pertains particularly to the possibility of occult viruses in insects. If the definition of an occult virus is to include ovarian contamination of the insect, the condition obviously exists, because adult insects must often be contaminated with virus. However, if occult viruses are to be defined as dormant elemental forms of the virus in a static state, intracellular in the host, not detectable by any known means, then their existence has not been proved; they may exist in some cases, but experimentation does not eliminate the possibility of extracellular contamination.

Cross infection with the nuclear polyhedrosis viruses is apparently possible between closely related species; however, very few studies in this area have been properly supported by serological identification of the viruses involved as well as by thin sectioning of the polyhedra from respective hosts to determine morphology. Generally speaking, the nuclear polyhedrosis viruses are more specific than the cytoplasmic polyhedroses. Cytoplasmic viruses cross-infect families of insects quite readily at moderate levels of dosage.

Although little work has been carried out with the granulosis viruses, they are believed to be highly specific for one host, and this is also true for the noninclusion viruses. However, the TIV, or Tipula iridescent virus (noninclusion), infects a wide range of hosts when injected but cannot invade and infect the same hosts by the oral route.

Methods of Propagation

Although insect viruses have for years been the most promising microorganisms for insect control, there has been no development of this potential beyond the point of proof of efficacy in limited field trials. This reticence is easily explained. These viruses are specific fastidious organisms that can be propagated only in the tissues of the living hosts. Many attempts have been made to cultivate viruses in insects reared in the laboratory or in the field on the natural host plants. However, this process required tremendous effort and coordination of facilities with available insect fodder, scrupulous care in preventing competitive diseases, and precise timing, since many of the insects reared for virus propagation were only available for a few weeks to a few months throughout the year.

Another technique used was to spray limited amounts of virus on a crop infested by a high population of the target insect and then collect the resulting dead and dying virus-infected insects from the field. There were several disadvantages to this method: (1) it was restricted to a short collection period; (2) there was no control of contamination by other insect pathogens, nor exclusion of possible undesirable biotypes that might harm man, animals, and plants; (3) effectiveness depended on the presence of high populations of the target insect, and this condition could not always be obtained. Further, the loss of the crop on which the insect was feeding had to be added to the cost of producing the virus.

Since about 1945, considerable progress has been made in rearing a number of insect species on semiartificial or completely artificial diets. The insects are mainly Lepidoptera, which includes some of the most harmful insect pests of forests and agricultural crops. There is little doubt that we will eventually be able to rear many of the Lepidoptera, phytophagous Hymenoptera, and some Diptera on variations of these media.

Once the technique of rearing a species on artificial or semiartificial media has been devised, it is a simple matter to produce viruses or any other fastidious microorganism in the host insect. There are several advantages to this method: (1) the production of the insect and microorganisms can be conducted throughout the year; (2) control of the extraneous biotypes associated with the virus in the insect can be more precisely managed, and, if necessary, such biotypes can be eliminated, although at some expense; (3) the control of competitive diseases is more feasible, since disease-free stock-lines of insects can be developed before they are introduced into the production area; (4) the initial infective dose can be precisely controlled (waste and expense are eliminated); and (5) environmental conditions can be held at optimum for production of virus, and bigger and better insects can be selected and reared (virus yield per larva is increased).

Disadvantages of the method are: (1) cannibalistic insects require separate containers or special rearing conditions to prevent loss of larvae (expense of rearing is increased); (2) we know little about the genetics and possible unconscious selection of the strains reared on artificial media, although there are no indications that virus produced on such insects is altered in virulence from virus obtained from larvae in the field; (3) stubborn, chronic infections of competitive diseases can be disastrous in such rearings; and (4) lines of insects tend to die out, possibly from a variety of physiological and nutritional reasons, and the dying out results in demands for reintroduction of new stock from the field, with all the inherent dangers of contamination through this practice. Despite all these problems, it is now possible to produce large amounts of virus at low cost.

Another problem to consider is the possibility of the target insect developing resistance to its specific virus. Preliminary studies suggest that the probability of the resistance developing to the extent of, or as quickly as, that which occurs with chemical insecticides is very remote. The virus has the advantage of the host through its enormous reproductive potential. However, if the virus produced is not replenished annually from different locations in the field, this advantage may be lost. It is essential that the virus produced for the coming year is taken from insects sprayed in the current year. This reduces the possibility of the insect in the field adapting to a standard strain of virus. There is no available proof that this can happen, but we have learned enough from our experience with resistance to insecticides and antibotics to take every precaution against a similar occurrence in work with insect pathogens.

The possibility of propagating insect viruses in insect-tissue culture is now a matter of serious consideration and experimentation. Several industrial groups in the world are producing vertebrate viruses in tissues grown in fermenter cultures holding several liters of medium. Although insect tissue-culture research has been making rapid strides since about 1950, there is little evidence that fermenter cultures of insect tissue are yet possible. Viruses have been grown in insect tissue, so this will not necessarily be a limiting factor once the proper insect-cell preparations and adequate media are developed. However, cultured cells invariably produce fewer polyhedra per cell compared with the equivalent yield from a living insect. This inefficiency may be a reflection of an inadequate medium.

Standardization of Preparations

The standardization of the polyhedrosis and granulosis viruses is still under investigation. However, some recommendations were made at the "International Symposium on the Identification and Assay of Viruses and *Bacillus thuringiensis* Berliner Used for Insect Control," which met under the auspices of the Organisation Internationale de Lutte Biologique (OILB) in London in 1964. It was recommended that such viruses (polyhedroses and granuloses) be standardized with reasonable accuracy by (1) counting the polyhedra or granules and (2) using a bioassay with healthy insects reared, if possible, on clean (preferably sterile) semiartificial media. Of course, each species of virus must be evaluated separately.

The viral polyhedra or granule counts can easily be made with a hemocytometer. However, there are obvious sources of error, such as the number and viability of particles in the polyhedron and the variability in size of polyhedra, that make it essential to conduct bioassay tests concurrently. The term "larval equivalent" has come into use in connection with the development of the *Heliothis zea* nuclear polyhedrosis virus. It was adopted to represent the average yield of polyhedra from one virus-infected last-instar larva of *H. zea*, namely, 6×10^9 polyhedra = 1 larval equivalent.

The bioassay should be conducted by depositing known numbers of polyhedra or granules, in sterile-water suspension, on the surface of or in media, or on the fodder used for the insect. The dose is usually expressed in terms of the number of polyhedra per unit of surface of the insect food treated. Thus, the number of polyhedra required to kill a certain percentage (LD_{50} preferred) of the test population in a given unit of time (usually 5 to 6 days) is the most desirable test.

The noninclusion viruses present a more difficult problem. Very little work has been done with these viruses, and a method of standardization (except by bioassay) is yet to be developed. However, it is suggested that carefully cleaned preparations of virus could be obtained by differential centrifugation and nitrogen. Also, DNA analyses coupled with injection of virus into a susceptible host might prove useful. Another possibility would be to develop a serological method based on the virus antigen titer per given weight of virus preparation coupled with bioassay by injection to estimate the amount of virus present.

Methods of Application and Use

There are two major methods of using viruses against noxious insects. One method involves the introduction of virus into a population of insects in carefully selected areas, usually determined by high population density. In certain insects, factors such as transovarial passage of virus and habits of colony feeding and extensive adult dispersal make possible the spread of the virus throughout the entire population in a remarkably short time. This method is most efficacious in treating large forest areas infested by high populations of injurious insects and has been particularly successful in treating species of sawflies in the family Tenthredinidae. However, this method should never be attempted without careful investigation of the insect to determine the precise character and progress of the disease.

In most species of insects there is no prospect of a virus disease overcoming the population by a single local introduction. Most insects susceptible to virus endure a chronic or endemic condition of the disease resulting from casual contamination by virus existing in the environment. This infection may often build up in a population over the course of a season, causing mass mortality late in the larval feeding stages. This mortality frequently occurs after major damage has been done to the crop on which the insect has been feeding.

In the second method of application, the virus is applied in a spray or dust in the same fashion in which chemical insecticides are applied. The application must be timed to coincide with the hatch of the insect, so that the larvae die early in their development, before major crop damage occurs. Fortunately, most first-instar larvae are more susceptible than the later instars to their specific viruses.

Next in importance to the timing of the application is the coverage of the plant. Most of the microbial agents must be ingested by the insect in order to kill. Thus, the dosage and coverage are interdependent criteria for successful control. Dosage of a pathogen for each insect species must be determined through experimentation in the field; laboratory findings usually cannot be directly translated to field dosages. However, field tests are dependent on laboratory standardizations of insecticidal activity. This activity, related to the weight of the material, is sufficient to determine the dilution in spray or in dust formulations required to ensure the proper coverage of the plant for effective insect control.

Coverage is the most crucial problem in spraying microbial agents on forest trees from the air because of the low volume of spray used for these operations.

To ensure that most forest insects receive a lethal dose of microorganism, the foliage should be treated when the insect is in its early instars and consequently is not feeding over a large area of leaf. The only solution to this problem is to concentrate the suspension of microbial agent to the utmost and apply the highest gallonage per acre that is economically possible. It is often necessary to allow newly formed leaves to open sufficiently to receive the spray; thus, the timing of the application must be precise. With experience and the proper organization of facilities and trained personnel, the results can be rewarding. However, the need for precise timing of application leaves the success of the whole spray program susceptible to the caprices of the weather. Heavy rainstorms during the optimum period for spraying can be disastrous unless proper provisions are made to incorporate into the formulation materials that permit the maximum adherence of the spray deposit to the leaf. Fortunately, sporeformers such as *Bacillus thuringiensis* and the polyhedra and granules of the viruses are compatible in combination with many of the “stickers” and “spreaders,” including fuel oil, as well as with several of the commonly used chemical insecticides.

Viruses are so specific that their use on a field crop may kill practically all of a given target insect without infecting the beneficial insect species on the plants. They are particularly useful when the target insect has built up a resistance to chemical insecticides. However, plant damage may still occur through attack by other plant-feeding species. In such an event, the virus might have to be supplemented by specific, quick-breakdown chemical insecticides to kill the remainder of the injurious insects on the plant.

The survival of the virus in the field is of utmost importance. Except for a few isolated cases, polyhedrosis and granulosis viruses apparently survive best under field conditions. Although there is no information on the effect of ultraviolet radiation on polyhedrosis viruses, it is thought that the polyhedron must protect the enclosed virus particles. More pertinent is the fact that viruses reproduce themselves in the insect, returning new fresh virus to the plant several days after initial treatment. This also enables the virus to reach plant surfaces that are untreated because of growth of the plant, thus maintaining good coverage.

A word of caution is necessary on the use of viruses. Mistakes have been made in the application of specific microbial agents by misdiagnosing the insect problem. Proper insect identification is essential in selecting the best microbial agent for control.

BACTERIA

Most of the bacterial insect pathogens used successfully in microbial control of insects are sporeformers. The production, storage, and subsequent use of bacteria that do not possess resistant stages have resulted in a high mortality of the microbes. The spores of the different bacteria currently in use survive all these processes quite readily. Various protective materials, such as casein and mucin, have been used to protect non-spore-forming bacteria from the environment in field use with a minimum of success. Accordingly, this discussion of bacterial pathogens dwells mainly on the sporeformers.

Taxonomy

The spore-forming bacteria fall in the family Bacillaceae, which has two genera, *Bacillus* and *Clostridium*. Both of these genera contain insect pathogens.

It is debatable whether the milky disease organisms, including *Bacillus popilliae* Dutky, *B. fribourgensis* Mille, *B. lentimorbus* Dutky, *B. popilliae* var. *australis* Beard, and *B. euloomarahae* Beard, really belong in the genus *Bacillus*. From close examination of several of these species serious consideration of their placement in the genus *Clostridium* might seem more appropriate. The matter deserves further study.

There has been some controversy regarding establishment of the species *Bacillus thuringiensis* var. *thuringiensis* as a separate taxonomic entity from *B. cereus;* however, the consensus among insect bacteriologists supports the use of separate species for the crystal-forming group of spore-forming bacteria.

Until the last decade, no recognized *Clostridium* sp. had been reported. However, this was corrected by the discovery of two species of the genus, *Clostridium brevifaciens* Bucher and *C. malacosomae* Bucher, both pathogens of tent caterpillars.

Methods of Propagation

Some of the spore-forming bacteria causing milky disease, exemplified by *Bacillus popilliae*, are fastidious and can be propagated only with extreme difficulty in artificial media. This group also includes the Clostridial pathogens of insects. Unfortunately, no one has managed to bring about complete sporulation of any of these bacteria in artificial media. Since the spore stage is required for the use of these bacteria in insect control, current methods employed in their production involve the introduction of the bacteria into living insects, either by injection or by feeding, whereupon the bacteria multiply to enormous numbers in the insect and are recovered by grinding up the host or using other appropriate extraction methods. This technique is still used to produce *B. popilliae* in the United States, and the product is available in commercial preparations.

Some of the less fastidious pathogenic organisms, such as *Bacillus cereus*, *B. thuringiensis*, and related crystal-formers, including *B. sphaericus*, can be propagated readily on artificial media of a fairly standard composition, including a balanced salt mixture, a protein source, and sometimes a vitamin and growth-factor source, such as yeast extract. These bacteria can be produced in fermenters of varying sizes, up to huge vats that contain 12,000 gal of medium. The sporulated organism is obtained either by vacuum-drying the whole nutrient medium with spores or by initial centrifugation to a spore slurry, which is eventually dried or stabilized for storage.

Mode of Action

During the course of their larval existence, most insects encounter food contaminated by bacteria. Since the insect gut is an excellent barrier against bacterial invasion of the hemocoel, most of these bacteria pass through the gut without causing any harm. A few bacteria produce agents that injure the insect or the larval gut in such a fashion that invasion of the body cavity follows. Such bacteria are considered "true pathogens." An understanding of the agents responsible for the invasive qualities of the bacterial pathogen is of utmost importance in the production of effective preparations and in the knowledgeable use of the bacterium in the field.

One of the most widely studied groups of pathogens is the *Bacillus thuringiensis* group. Research on the mode of action has shown that these bacteria produce at least four substances toxic to insects. These are: (1) a proteinaceous, crystalline parasporal body capable of paralyzing the gut of most lepidopterous larvae; (2) a small, dialyzable molecule that is heat stable and soluble produced outside the bacterial cell in the surrounding medium, and that affects larvae and pupae of Diptera and apparently kills some Lepidoptera; (3) phospholipase C, an enzyme that is produced by the growing cell and breaks down essential phospholipids in the insect cell; and (4) another unidentified phospholipase that affects phospholipids, probably releasing fatty acids from the molecule. Production of an effective bacterial preparation, based on *B. thuringiensis*, must be arranged so that the active crystal toxin and viable spores are produced. Since the manner of production can influence the activity of both these essential components, their identity and means of assaying their activity are necessary to manufacture a reliable, standard preparation for insect control.

Nothing is more important to an informed approach to insect control through the use of bacteria than the mode-of-action studies on each potentially useful bacterium. Much remains to be investigated in this area. A few species of bacteria, including strains of *Serratia marcescens* Bizio, *Pseudomodas aeruginosa* (Schoeter) Migula, and some of the Micrococcaceae, have no ability to invade but can kill insects if they gain entrance to the hemocoel through an artificial breach (a wound or tear) in the gut. Acute damage of this type is rather common in hard-shelled insects that lead a very active life, such as cockroaches, grasshoppers, crickets, and some beetles. Such microorganisms have been described as "potential pathogens." They can kill insects when introduced into the body cavity in low numbers but other similar bacteria are quickly eliminated from the hemocoel even when introduced in large doses. Much research is needed in this regard.

Standardization of Preparations

Standardization of nonfastidious bacterial control agents is most properly carried out by microscopic counts of cells or spores in suspension (counts in which blood cell count chambers are used) combined with plate counts to determine the number of viable units present. These counted suspensions are fed by forced gut injection, or on the surface of fodder, to susceptible insect larvae, and the LD_{50} of the test insect is determined under standard conditions. The findings are usually compared with results obtained by using a pretested standard preparation of the bacterium; thus some of the variation encountered in insect populations is eliminated.

Fastidious organism, such as *Bacillus popilliae*, can be standardized by microscopic counts coupled with feeding tests or by injecting counted suspensions of cells into the hemocoel.

Methods of Application and Use

Bacteria may be applied in carefully selected sites, where they are colonized and spread through the insect population. Ultimately they provide permanent control. An example of this type is the organism *Bacillus popilliae*. However, most of the bacteria currently recommended for insect control must be applied as regularly as chemical insecticides and must blanket the crop with sufficient concentration of the organism to cause high mortality in the target species of insect.

Bacillus thuringiensis can be applied in water suspensions, oil–water emulsions, bacterial powders extended with clay, and granular formulations with clay, the choice of materials depending on the target insect. There is strong suggestion of a correlation between the latitude and the effectiveness of dusts as opposed to water sprays. Dusts formulated with *B. thuringiensis* are apparently more effective than wet formulations in Texas and southern California. Such dusts are also more effective in these southern areas than in the northern part of the country. This may mean that dusts protect the bacterium from the more direct angle of solar radiation in southern climates.

The creation of an acidic reaction in wet spray mixtures seems to enhance the effect of *Bacillus thuringiensis* against several insect species tested. This phenomenon is not completely understood, but it may involve the inability of the spore to germinate at a lower pH and a consequent tendency for the spore to stay in spore form longer while exposed to the environment.

Again, as in the viruses, the microbial agent is like a chemical stomach poison in that it must be ingested to kill. Consequently, proper timing of application and coverage of the plant to ensure the consumption of a lethal dose is of paramount importance to obtain rapid, decisive control.

PROTOZOA

The protozoa kill enormous numbers of insects either directly or by reducing the fecundity of the adults. It would be improper not to acknowledge their importance in the field, but it is not expected that they will be used extensively for insect control until much more is known about their potential. Most protozoa do not act decisively; they kill slowly, if at all; they prolong the larval life of the insect in the field, thus exposing the insect longer to predators and parasites, and they reduce the fecundity of surviving adults. They are often associated with other insect pathogens, particularly the viruses, and it would be worth knowing whether the protozoa might not predispose insect larvae to infection by a virus. There are some reservations concerning their proposed use in insect control. Certain of the Microsporidia can cause diseases in fish and mammals, and any protozoan recommended for dissemination in the field should be rigorously tested for safety to these animals.

Taxonomy

The protozoa affecting insects belong to the classes Sarcodina (the amoebae); the Mastigophora (the flagellates); and the Sporozoa, including the Gregarinida (the gregarines and the Eugregarines), the Coccidia, and the Microsporidia (a very important group of invertebrate, fish, and mammalian pathogens).

The identification of protozoa affecting insects is generally poor. There is little justification for naming new species on the basis of host isolations, when further tests indicate that the protozoan lacks specificity and will at times cross-infect families and even orders of insects. Furthermore, the criteria (mainly morphological) used to designate species are inadequate and misleading. There are many sophisticated methods of identification now available to taxonomists in this field; these include serological methods, RNA–DNA–residue phosphorous analysis, and base-pair analysis.

Methods of Propagation

Only a few species of protozoa from insects have been propagated on artificial media, namely, *Tetrahymena pyriformis* (Ehrenberg), *T. chironomi* (Warren), and *Crithidia fasciculata* (Léger). This means that large quantities of other protozoa can only be obtained from culture of the insect. Very few attempts to produce and use the protozoa as insect control agents have been made, even though this pathogen can be propagated in large numbers by using the techniques that are used for producing viruses. Recent work in Czechoslovakia has stimulated some interest in this aspect of microbial control.

Standardization and Methods of Application

Protozoa can be standardized by microscopic counts of the spores or cells coupled with bioassays of suspensions of them and by using susceptible insects. There has never been an alternative method to the bioassay for determining the viability of stored spores, and, in many cases, the reduction of viability of resting stages of sporozoa is an accepted fact. Consequently, there is no possibility of a standard preparation for comparison in bioassaying these pathogens. Much work could be profitably expended on the growth and storage of protozoan pathogens.

So few experiments have been done with protozoa in field dissemination that there is little to discuss, although the possibility of mass-producing tetratrymenid ciliates to use in experimental control of certain species of tropical mosquitoes should be thoroughly investigated. The use of resting stages, such as spores in water suspension, is the only method tried in the past. The compatibility of protozoan spores, particularly the microsporidia, with extenders, wetting agents, and stickers, is open to serious question because of the effect of chemicals in the laboratory on the viability of spore suspensions.

FUNGI

Many attempts have been made to use fungi to control insects. Observations of insect populations for many years have shown that the fungi are important, effective pathogens of insects in nature. However, fungi are dependent to a high degree on local weather conditions and the microenvironment in the vicinity of the target insect. For this reason, they have been unreliable in most cases. Attempts to colonize fungi in insect populations usually failed. Attempts at direct control by blanketing crops or areas with resting stages of fungi were only infrequently successful, and the replication of these successes in subsequent years often failed. The consensus of insect pathologists is that fungi will not be used successfully in the field to control insects, because of our inability to control the host environment.

Taxonomy

The statements made concerning the identification of protozoa apply equally to the fungi. There is less excuse for the heavy use of morphological characteristics in the mycology of insects than there is in protozoology, since most of the species of fungi affecting insects are saprophytic and can be grown on artificial media. There is a whole field of endeavor here for the interested investigator. The fungi belong to the Thallophytes, and the entomogenous fungi occur in all four classes, Phycomycetes, Ascomycetes, Basidiomycetes, and the Deuteromycetes or Fungi Imperfecti. The Deuteromycetes contain the fewest species of pathogens, and the Phycomycetes (Entomophthoraceae, Coelomycetaceae) and the order Hypocreales of the class Ascomycetes contain most of the entomogenous species.

Standardization and Methods of Application

Nonfastidious fungi can be standardized in much the same fashion as spore-forming bacteria. Spore counts and bioassay are adequate. The difficulty in establishing reliable standards can be partially offset by colony counts in which plating techniques are used. Some of the fastidious fungi, such as the Entomophthoraceae, are difficult to assay because of the inability to determine viability of the spores. Investigations leading to the propagation of these organisms on artificial media are badly needed.

Many species of entomogenous fungi can be propagated in huge amounts on artificial media. However, these fungi are so variable, and so little is known about their mode of action, that production of most species is an empirical affair. Mode-of-action and invasion studies are the prerequisites of knowledgeable production of these organisms.

Several species of fungi are fastidious and must be produced on the host. This procedure gives better assurance of obtaining truly pathogenic strains and presents a reasonably effective method based on our increasing knowledge of methods of rearing insects.

RICKETTSIAE

The rickettsiae have recently been noted to kill insects in several parts of the world. For a variety of reasons, however, it is unlikely that they will ever be used as insect control agents. The rickettsiae require from several weeks to months to kill the host and are not considered appropriate for rapid, decisive insect control. Furthermore, isolates of these pathogens are capable of growing in mammalian-tissue culture and have caused death when injected into white mice. It would be highly improper, therefore, to consider their wide dissemination in the field, because of the hazards imposed on other biotypes in the environment.

NEMATODES

Approximately 1,500 insect species have been reported as hosts to a variety of round worms, or nematodes (Nemathelminthes). Most of these nematodes severely damage the host insect and usually kill it.

Taxonomy

Nematodes invading or semiparasitic on insects belong to the classes Nematoda, Nematomorpha, and Acanthocephala. Most of the obligate parasites of insects fall in the families Mermithidae, Tetradonematidae, and Allantonnematidae. Of these, the mermithids have received the most attention.

Some nematodes (particularly the genus *Neoaplectana*) can develop in the host after its death; thus, they are considered semiparasitic. The resulting progeny, as ensheathed second-instar larvae, break out of the host cadaver and survive as free-living entities, as long as moisture is present, until they encounter a new host.

Propagation and Use

The *Neoaplectana* have been studied in some detail in relation to production on artificial media. *Neoaplectana glaseri* Steiner was mass-produced on artificial diet (fermented potato mash with infused veal pulp) for experiments in controlling the Japanese beetle, *Popillia japonica* Newman. Another species known as DD 136 (or "Dutky's nematode") has been produced on a nutrient agar with pork kidney and on the living larvae of the greater wax moth.

The DD 136 nematode carries with it a bacterium that grows in the blood of the invaded insect. The nematode feeds on the bacterium, and in turn the bacterium provides an antibiotic that discourages secondary invaders. Since the bacterium does not require oxygen, the entire supply is left for the nematode's use. This nematode, originally isolated from the coding moth, can attack and kill more than 45 species of insects. It would seem that such a organism would have tremendous potential for insect control, yet field experiments using DD 136 have not been very successful. Part of the explanation for this may be improper handling of the organism in the field. However, the nematodes are not easily stored, and their requirements for moisture and oxygen are quite critical. Much more work will be necessary before nematodes are easily produced, stored, and used in the field with confidence.

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CHAPTER 9

Management by Genetic Principles

Genetic principles have been employed by man for centuries to develop varieties and strains of plants and animals more suited to his purposes than were their progenitors. The success of the method is illustrated by the diversity of highly specialized varieties of plants and animals available for use in modern agriculture. Much of the foundation of modern genetics rests on principles developed through studies of an insect—the fruit fly, *Drosophila melanogaster* Meigen. The silkworm, *Bombyx mori* (Linnaeus), and the honey bee, *Apis mellifera* Linnaeus, have also been objects of intensive genetic studies for several decades. These studies have accounted for the development of improved varieties of these economically valuable species as well as for a wealth of genetic knowledge.

Despite impressive evidence that genetic principles can be applied effectively in modifying insect populations, this approach has not received much consideration from entomologists. Little attention has been devoted to the possibility of reducing insect numbers by self-destroying changes in the innate qualities of individuals of a population, which might be induced by the application of genetic principles. Also, the possibilities of improving the pest-destroying capacities of insect predators, parasites, and pathogens have been little exploited. Success in the application of the sterile-male technique for insect control, treated in detail in Chapter 15, has stimulated interest in and opened new avenues for study of genetic manipulations in insect-pest populations leading to their control. In retrospect, it is surprising, and rather disappointing, that the genetic principles so effectively applied in other phases of modern agriculture have not found greater application in pest management and control, since the underlying principles are the same.

A number of features of insects suggest that they should be widely susceptible to control by the application of genetic principles. Their high biotic potential and short life cycles make selection possible from large numbers in a short time. Developments during the last few decades have made possible the mass-rearing of many species in numbers large enough to inundate natural populations. Live insects can readily be stored, transported, and disseminated over large areas. Numerous biotypes or races, from which selections can be made, occur naturally. Their genetic plasticity has been impressively demonstrated by the rapid and widespread development of resistance to insecticides in the populations of about 200 species. This adaptation involves modifications in behavioral, morphological, and physiological characteristics, all of which are under genetic control. The few intensive genetic studies of insects, such as those on *Drosophila*, the silkworm, and the honey bee, have produced abundant evidence that genetic manipulation could be a useful technique in pest management.

ALTERATION OF "FITNESS"

INCREASING FITNESS

Outstanding examples of modifying the innate qualities of insects to man's advantage come from work on the silkworm and the honey bee. In both cases, basic objectives have been the same as those involving cultivated crops and domestic animals, viz., improving yields of specific requisites.

Japanese research on genetics of the silkworm has provided the most thoroughly documented information available on the possibilities for genetic modification of insect populations. Unfortunately, much of the intensive research on the genetics of the silkworm has been published in Japanese and consequently has not received the attention it deserves. The maternal inheritance of univoltine, bivoltine, quadrivoltine, and multivoltine races in the silkworm has been known for more than 50 years. Voltinism is controlled by three sex-linked alleles and three autosomal alleles. Epistasis is complete for the sex-linked genes, and the autosomal genes have a cumulative effect proportional to the number of dominant genes. Univoltine females produce hibernating eggs; multivoltine females produce nonhibernating eggs; and bivoltine females produce hibernating eggs if they have been incubated at a high temperature (25°C) and nonhibernating eggs if they have been incubated at a low temperature (15°C).

The number of molts is determined by several genes. There are four molting patterns: (1) tetramolting–standard type, larva spins cocoon and pupates after the fourth molt; (2) trimolting–most common type in primitive races and in the wild silkworm, simple dominant to tetramolting, larva passes through three molts before spinning cocoon; (3) pentamolting–larva spins a cocoon after passing through five molts; and (4) recessive trimolting—which in crosses with pentamolting strains produces only tetramolters in the F_1 generation, but F_2 progeny segregate into trimolters, tetramolters, and pentamolters.

The inheritance of cocoon and silk characters has been investigated in crosses of univoltine or bivoltine races with tetravoltine and multivoltine races. Sex linkage was established for such quantitative characters as duration of larval life, pupal weight, and weight of cocoon layers; autosomal genes also affected expression of these characters. The amount of floss silk enclosing the cocoon was at least partially influenced by a gene on the Z chromosome. Genes for "superior-neatness" and "lousiness-free" characters of raw silk were incompletely dominant to those for "inferior-neatness" and "lousiness-rich" genes; open cocoon was incompletely recessive to normal; and thinness of cocoons in the equatorial region was incompletely recessive. "Stained cocoon," a rusty or dark rusty color from the inside, was caused by a weak acidic fluid excreted by the malpighian vessels during spinning.

The wide and early application of the principle of heterosis in silkworm culture has been matched only by that in corn. The practical value of heterosis was known to European silkworm producers as early as the middle of the nineteenth century. In the F_1 generation of crosses between widely different parental strains of silkworm, the rearing period is shorter, mortality is lower, cocoon fiber is longer and thicker, reeled fiber weight is heavier, and the percentage of double cocoons is higher than in averages of the parental strains. Silk producers now use F_1 hybrids exclusively.

Breeding techniques that had so successfully modified domesticated plants and animals were initially disappointing in the honey bee, in spite of the tremendous amount of variation existing among races and strains of the species. The honey bee has remained essentially wild after more than 5,000 years of culture. Genetic studies during the last few decades show that inbreeding has been one of the major reasons for the limited success of selection techniques in improving the honey bee. Inbreeding brings together similar lethal alleles and lowers brood viability, colony population, and honey production. However, significant accomplishments in improving honey bee strains have been made by replacing the German race with importations of superior stocks of Italian and Caucasian races.

The use of isolated mating yards for control of male parentage made possible the next significant advance in bee-breeding. This technique resulted in the development of strains of the honey bee with high levels of resistance to diseases such as American foulbrood, *Bacillus larvae* White, and acarine disease, *Acarapis woodi* (Rennie).

The perfection of artificial-insemination techniques set the stage for rapid progress in honey bee-breeding. Artificial insemination has made the development and maintenance of inbred lines and controlled hybridization rather simple procedures. Hybridization of inbred lines of known constitution has become a practical means of improving honey-producing ability, pollinating ability, wintering ability, and disease resistance. It is also effective in changing size, color, proboscis length, and tractability in the honey bee.

The application of genetic methods for improving the potential of parasitic insects began in the early 1940's, when the temperature preference of a laboratory strain of *Dahlbominus fuscipennis* (Zetterstedt), a parasite of the European spruce sawfly, *Diprion hercyniae* (Hartig), was almost completely reversed after four generations of selection, and a laboratory culture, in danger of being lost because of a rapidly declining ratio of females to males, was saved by outcrossing and rigid selection of progeny for high female production. By use of this technique, the percentage of males being produced was drastically reduced, and the mean number of progeny per female was doubled.

Experiments with *Horogenes molestus* (Uchida) provide convincing evidence of what can be done toward improving the potential of insect parasites by the application of selection techniques. The host preference of this species, normally a parasite of the oriental fruit moth, *Grapholitha molesta* (Busck), was modified to the extent that the parasite would accept a foster host, the potato tuberworm, *Phthorimaea operculella* (Zeller). Initially, the parasites could not be made to accept the tuberworm except by the use of attractants to induce oviposition. However, after 11 generations, a strain was selected that did not require use of the attractants. With 39 generations of additional selection, a strain was developed that was 24 times as efficient as the original.

Any of the selective breeding techniques of plant and animal breeders may be used to improve the adaptations of parasitic insects. For example, interspecific crosses may provide greater genetic variability in stocks undergoing selection. The difficulties inherent in maintaining the integrity of new stocks must be recognized as well as the possibility that in modifying one character favorably, others may become unfavorable.

The potentialities for increasing germ-plasm diversity within cultivated plants through hybridization with wild ancestral forms and relatives have been recognized and used widely in plant-breeding. Full exploitation of the potential of interspecies and intergeneric crosses in plants has been limited by hybrid sterility, hybrid inviability, and close linkage of undesirable genetic factors with desirable ones. These difficulties have been overcome to some extent by the use of colchicine to double chromosomes, refinements in the technique of culturing excised embryos, and breakage of chromosomes between desirable and undesirable genes by irradiation. Tapping the gene pool of related species for characters not available intraspecifically is feasible among insects as well as plants. Virtually every study involving attempted crosses between closely related insect species has demonstrated the possibility of some degree of gene exchange. Crossbreeding and backcrossing experiments with stink bugs, *Euschistus* spp., and spider mites, *Tetranychus* spp., demonstrate conclusively that there are no technical reasons to prevent the transfer of a wide variety of useful characters across species boundaries where they may be combined as desired to form strains with superior or inferior adaptation to the environment.

Rapid adaptation of insect pests to insecticides, commonly referred to as insect resistance to insecticides, has stimulated a considerable amount of research in insect genetics and provides further evidence for the possibilities of modifying insect populations through the application of genetic techniques. The major effort in this area has dealt with analyses of the genetic factors involved in the phenomenon, but the possibility of restoring insect susceptibility to insecticides has been considered.

A major problem involved in the expanding use of insecticides for the regulation of pest populations has been the adverse effects of the chemicals on parasitic and predacious species. The obvious possibility of developing highly resistant strains of these beneficial insects for release in treated areas has been considered as a solution to the problem, but little effort has been devoted to such an approach. Selection in the field has occurred, however, and resistant strains of biological control agents have developed parallel to the development of resistance in pest species. In laboratory experiments, a substantial increase was developed in the tolerance to DDT of a laboratory strain of the important oriental fruit moth parasite, *Macrocentrus ancylivorus* Rohwer, after it had been exposed to selective dosages for a period of 9 months.

DECREASING FITNESS

Apparently, the first attempt to control a pest by the application of genetics to decrease fitness had to do with tsetse flies, *Glossina* spp. Interspecific crosses were made of *Glossina swynnertoni* Austen and the reproductively but not sexually isolated *G. morsitans* Westwood. Viable but sterile offspring were obtained from such crosses, which competed with normal individuals for the requisites for survival in the environment. Although the method seemed to offer promising leads, it was not developed further. Crosses between "weak" and "strong" races of the gypsy moth, *Porthetria dispar* (Linnaeus), which give rise to sterile intersexes, have been suggested as a means of decreasing the fitness of populations of this pest.

Other sterility mechanisms may be useful in pest control. Among these are an insemination reaction characterized by formation of a hard mucoid plug to block the vagina of the female, typical of many species crosses in *Drosophila;* sterility factors causing unilateral incompatibility between populations of *Culex*; sterility in male progeny of many strain crosses illustrated in *Anopheles*, in which crosses between types in either direction result in fertile females and sterile males in the F_1 generation; and maternally inherited sterility of males in *Drosophila melanogaster*, in which all male offspring are affected.

Incompatibility between populations of species complexes of mosquitoes, e.g., the northern house mosquito, *Culex pipiens pipiens* Linnaeus, or *Aedes scutellaris* (Walker), is caused by cytoplasmic factors. Within the *C. pipiens* complex, at least 15 crossing types exist; copulation and insemination occur in all cases. However, in some crosses, fertile offspring are produced, but with reciprocal crosses the offspring are sterile. Sterility is caused by an unknown cytoplasmic factor transmitted to the egg, which kills the incompatible sperm after it has entered the egg, but prior to karyogamy. Thus, with this mechanism, control of a particular insect population could be effected by mass-rearing of males of one crossing type and releasing them in an area containing an incompatible crossing type. In the use of this method, it would be essential that no females of the incompatible strain be released.

It has been demonstrated, especially in mosquitoes, that appropriate crosses of two different species or races of insects will produce fertile females and sterile males in the F_1 generation. The sterile males have atrophied testes and are aspermic but have normal sexual behavior. With this technique, sterile hybrids could be reared and released, or the males of one species could be reared and released in an area containing females of a different species. Either procedure would produce the desired hybrids and sterility.

The above two techniques relating to the genetics of mosquitoes have the great advantage of being selective and leaving no toxic residues. They should be used only when natural populations are low, or when numbers can be depressed by judicious use of insecticides, water management, or other practices that reduce mosquito-breeding.

Cytoplasmic incompatibility and hybrid sterility are only two examples of genetic mechanisms for inducing sterility in a natural population. Other possibilities that should be considered are conditional lethals, which include seasonal and population-density lethal factors, unisexual lethal mutations that affect only one sex, and sex-ratio alterations such as the male-producing factor in mosquitoes.

Certain strains of the yellow-fever mosquito, *Aedes aegypti* (Linnaeus), demonstrate the possibility of rendering a population unadapted to a particular environment. Larvae of an intersex-producing strain from Kenya, inbred by single-pair brother–sister mating for 17 generations, produced normal adults in a 1:1 sex ratio when reared at 27 to 28°C; when reared at 30 to 34°C, half of the adults were normal females, but the other half were intersexes; and larvae reared at 35 to 37°C gave morphologically female adults. The behavior of converted males (phenotypic females) resembled normal females with respect to mating and insemination but produced no eggs. This type of behavior was caused by a single gene, recessive, autosomal, and sex-limited in expression. In tropical species, sterility conferred by such a heat-sensitive gene would be highly deleterious to a population.

Many lethal genes exist in populations of insect species that have been subjected to genetic analyses. They occur at similar frequencies in populations of most pest species. The number available for use in control programs is apparently limited only by the amount of effort and imaginative research devoted to finding them. Deleterious genes need not be lethal nor act immediately for effective control. Drastic reductions in insect numbers can be obtained theoretically by constant low-level mortality factors superimposed on populations already exposed to the stress of adverse environmental conditions, as, for example, low temperatures during hibernation. Three requirements are essential to the success of control measures utilizing the release of strains carrying unfavorable genetic characters: the factors must not prevent rearing under laboratory conditions; they must not interfere with mating ability; and they should act at particular times, such as during hibernation or immature stages. It has been postulated on theoretical grounds that the eradication of the boll weevil, *Anthonomus grandis* Boheman, could be achieved in a few years if males carrying two lethal genes were repeatedly released into field populations.

Although the sterile-male technique also is a self-destruction or autocidal method, it does not properly come into consideration under genetic control, because complete sterility cannot be inherited in populations, whereas lethals and similar deleterious genes can be inherited under certain conditions.

The advantage of using lethal genes over the sterile-male technique is that heterozygous individuals for the lethal character continue to breed in the treated population for some time after their release. Ideally, a lethal gene carried in the heterozygous condition should be linked to some characteristic that has survival value to natural populations. It would persist in such a state but would not remove more than 25% of the pest population.

Although the genetics of voltinism are best understood in the silkworm, the phenomenon also occurs in other species. The European corn borer, *Ostrinia nubilalis* (Hübner), is an outstanding example. Univoltine and multivoltine strains of this pest occur in many areas of its distribution. If the factors responsible for univoltinism could be fixed in natural populations, the damage potential of this pest could be greatly reduced. Such a population-controlling factor superimposed on the heavy mortality that usually occurs during hibernation could virtually prevent the species from attaining pest status in many areas. Conversely, if factors could be found to prevent the insect from diapausing, and if these factors could be fixed in natural populations, the species could be eliminated. The corn borer, like most other insect species, relies on diapause as the only mechanism for existing during periods when environmental conditions are totally intolerable otherwise. This approach has practical possibilities in the case of the field cricket, *Teleogryllus commodus* (Walker), in Australia. Northern populations there produce nondiapausing eggs that cannot survive the southern winter. By crossing females of the southern diapausing strain with males of the northern nondiapausing strain, eggs are produced that cannot survive the southern winter. The effects of releasing northern males in inundative numbers into an area populated by southern strains should be as effective, theoretically, as the sterile-male technique.

Seasonal lethals and density-dependent factors are especially promising for potential use in manipulating pest populations. Use of such factors would require that advantage be taken of natural fluctuations in population cycles in timing the introduction of any deleterious genes into a target population.

PROSPECTS FOR GENETIC CONTROL

Autocidal methods offer one of the most powerful means of reducing populations of pest species. Major advantages of such a method over other methods of regulating animal populations are as follows: (1) effects exerted on untreated individuals of the interbreeding group; (2) rapidity with which effects can spread throughout a population; and (3) lack of any immediate biological defenses with which susceptible individuals can oppose the method.

Probably one of the major reasons entomologists have devoted so little time to the application of autocidal techniques to pest control has been the difficulty of incorporating deleterious genes into field populations. This still poses a real barrier to full utilization of the method. Insects have been remarkably successful in developing various homeostatic mechanisms that prevent catastrophic deleterious effects of the new environmental hazards on their populations. There is no evidence suggesting the loss of their evolutionary adaptability. However, recently developed methods and technology of rearing huge numbers of insects in the laboratory for release into natural populations greatly improves the potential for the genetic control of insect pests. Huge numbers of such species as the screw-worm, *Cochliomyia hominivorax* (Coquerel), melon fly, *Dacus cucurbitae* Coquillett, oriental fruit fly, *Dacus dorsalis* Hendel, Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), and Mexican fruit fly, *Anastrepha ludens* (Loew), have been produced and released into natural populations on a scale large enough to demonstrate practicability on any scale that might be required in distributing and maintaining lethal genes in a target population. Methods have been devised for rearing many other species in the laboratory on semisynthetic diets, for example, the fall armyworm, *Spodoptera frugiperda* (J. E. Smith); cabbage looper, *Trichoplusia ni* (Hübner); sugarcane borer, *Diatraea saccharalis* (Fabricius); boll weevil, *Anthonomus grandis* Boheman, *Heliothis* spp.; and the mosquitoes, *Aedes aegypti* (Linnaeus), *Culex* spp., and *Anopheles quadrimaculatus* Say. Such methods have progressed to the point that only development of the engineering phases of large-scale rearing programs would be required to yield individuals of the desired genetical constitution in numbers great enough to inundate target populations in large areas of their known distribution. Success of the sterile male-release technique for control of the screw-worm has demonstrated the practicability of the method of inundating populations with genetically deficient individuals.

Heterosis and meiotic drive may prove to be the most useful mechanisms for propagation of deleterious genes in insect-pest populations. Heterotic factors are carried in populations, in some cases, even though they are disadvantageous as homozygotes. Evidence of the preferential segregation of one gamete at the expense of the other is increasing. Distortion of segregation ratios brought about by meiotic drive gives an advantage to the chromosome or locus that has it. Chromosomes or loci exhibiting meiotic drive occur disproportionately often in the gametes contributing to each generation and tend to increase in each generation. Thus, a few individuals introduced into a population would have their chromosomes pass into the genetic makeup of the whole population. The phenomenon is thought to be widespread, and there is no reason to doubt that it can be manipulated.

Genetic techniques apparently offer great possibilities for increasing the effectiveness of insect pathogens. For example, various species of muscardine fungi, *Spicaria* spp., are spectacularly effective in the control of larvae of such important lepidopterous pests as the cabbage looper, *Trichoplusia ni* (Hübner), and a related species, *Pseudoplusia includens* (Walker), the green cloverworm, *Plathypena scabra* (Fabricius), and the velvetbean caterpillar, *Anticarsia gemmatilis* Hübner. However, in the southern United States these pathogens rarely exert any appreciable effect on populations of the pests until late summer or early fall, usually coincident with a period of cool wet weather. Frequently, unacceptably high population levels of one or more of the pests are reached before the pathogens become effective. This suggests the possibility that strains of the fungus might be selected that could operate more efficiently in a wide range of environments. Such an approach deserves investigation. Application of genetic methods for improving insect predators, parasites, and pathogens in all the characteristics contributing to their effectiveness as biotic regulators of pest populations offers great opportunities in the control of harmful species. Numerous geographical and biological races of parasitic species exist in nature, and they differ in their potential value as biological control agents. For example, *Paratheresia claripalpis* Wulp, a tachinid parasite of the sugarcane borer occurs in highly variable races. The species is indigenous to South and Central America, Mexico, and parts of the West Indies. Stocks from Trinidad have been introduced successfully into the islands of Dominica and Guadeloupe, and into Florida. In the islands it has become an important parasite of the sugarcane borer, but in Florida it is of no economic importance. A comparison of adults of stocks from western Mexico and Trinidad shows that those from Mexico are much larger, have pupal periods of 12 days compared with 8, and produce many more larvae than those from Trinidad. There are also marked differences in host adaptation between the two races. Both breed successfully on the sugarcane borer, but on the related species, *Zeadiatraea lineolata* (Hampson), only about 2% of the larvae of the Trinidad race develops successfully; the Mexican race does as well on *Z. lineolata* as on *D. saccharalis*.

Obviously, enough genetic diversity exists in *Paratheresia claripalpis* to offer the possibility of developing a strain as effective in parasitizing *D. saccharalis* in Florida as in Guadeloupe. Two approaches in the application of genetic principles to such an objective offer possibilities: (1) select stocks of the maximum possible genetic variability for release in the specific environment and rely on the forces of natural selection to develop an effective strain, and (2) develop races or strains in the laboratory that can operate effectively in environments unsuited to existing strains; this may be done by hybridization, irradiation, or other means of enriching the gene pool.

Application of genetic techniques should also prove helpful in the increasingly important area of sex-attractant research. One of the great difficulties of research in this field is that the specific chemicals involved occur in such minute quantities in the insects being studied. Application of the same breeding techniques used to increase the yield of milk per cow or eggs per hen should result in equally impressive increases in yield of sex attractant per female sugarcane borer, for example.

Like all other methods practiced or proposed for insect control, the application of genetics may also have some undesirable features. The most serious of these, perhaps, is that the introduction of new genes into field populations could provide additional variability, from which more destructive pests might evolve. However, most pest species are already so highly plastic that the addition of a few more genes should cause little concern. Any unexpected problems should show up in field trials in limited areas. The frequently voiced argument that the target species will evolve mechanisms allowing it to resist genetic control measures may be dismissed on the grounds that this probability causes genetic control to fall into the same category as all other techniques proposed for insect control.

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CHAPTER 10

Cultural Control

The principle involved in the cultural control of insect pests is purposeful manipulation of the environment to make it less favorable, thereby exerting economic control of the pests or at least reducing their rates of increase and damage. The development of cultural control methods requires a thorough knowledge of the life history and habits of the insect and its plant or animal host. The most vulnerable stage or stages of the insect pest's life cycle must be determined, and farming, storage, or forestry practices must be altered to prevent attack, kill the pest, or slow down its rate of reproduction. Proper modification of farming methods has controlled many species of insects. When these control methods are also desirable agronomic practices, they usually are readily adopted. However, when cultural controls are poor agronomic practices, the advantages and disadvantages must be weighed carefully before the methods are recommended. Cultural control methods are often economical and dependable, although seldom spectacular, and may require long-term planning for greatest effectiveness.

Cultural control measures, such as modifications of the planting, growing, cultivating, or harvesting of crops, are aimed at prevention of insect damage rather than destruction of an existing infestation. The methods must usually be employed long before damage becomes apparent, and it is often difficult to evaluate their effectiveness. It may be easier to control some insects in a stage in which they are doing no damage than in the stage in which they are serious pests. Cultural control practices are often more effective if practiced throughout a given area. This is especially true for insects that migrate a considerable distance.

Since cultural control methods are usually based on modifications in the time and manner of performing necessary operations in the production of a crop, they are usually among the cheapest of insect-control measures. Although cultural practices alone may not give completely satisfactory insect control, they are important in minimizing injury and protecting the crop and should be considered in any integrated control program. Sometimes a slight population reduction brought about by cultural practices delays buildup to damaging levels. In other cases, if good cultural practices are followed, a reduced number of insecticide applications may be adequate for control.

SANITATION

Sanitation to prevent or reduce insect infestation through removal of breeding and hibernating sites is a sound insect-control principle that has broad applicability. The user must be familiar with the habits of each insect species to apply a sanitation method of control at a time when it will be most effective. Accordingly, much research needs to be done on the biology and ecology of many insect pests, with special attention to hibernating stages, in order to foster use of this method of control. Sanitation practices, which include utilization or destruction of crop refuse, are often an economical, effective way to control insects. In addition, they result in a generally cleaner, healthier environment. The tremendous gains resulting from the extensive use of economical and effective insecticides has caused a retrenchment in the practical use of many sanitation measures.

PLANT AND CROP REFUSE UTILIZATION OR DESTRUCTION

Destroying insect-infested plant or crop refuse usually helps prevent damage to future crops. However, the advantages and disadvantages of total refuse destruction within a field must be considered, since wind erosion of soil, water runoff, and soil-moisture loss by evaporation may increase on land where all refuse has been burned or turned under. It may not be necessary to destroy or plow under the refuse completely. Sometimes the refuse can be broken into small parts, or the roots of plants can be dug up and allowed to decompose on the surface of the soil. Collecting and destroying fruit drops, a sanitation method that kills some pests, is a preventive method of control. It eliminates both insects and diseases and is especially applicable to small isolated orchards of a few trees; however, the procedure is impractical for commercial orchards. Pasturing of livestock at the right time can be an effective method for destroying insects in crop remnants. The destruction of abandoned orchards and of slash following logging operations in the forest prevents future outbreaks of certain injurious insects.

Agricultural Crops

Control of the boll weevil, *Anthonomus grandis* Boheman, includes fall destruction of infested plants of cotton, *Gossypium hirsutum* L., as soon as possible after harvesting but prior to the first killing frost. This will also provide a better seedbed the following spring. Results of large-scale demonstrations conducted in Texas have proved the advantages of early-fall stalk destruction. In a county-wide stalk-destruction program in Texas, the fall boll weevil population was greatly reduced, and the infestation reached only 27% punctured squares by late July the following season. In an adjoining county, where no fall clean-up program was carried out, the infestation reached 63% punctured squares by the same date in July. An infestation level of 27% may cause little or no reduction in yield of cotton, but 63% infestation is likely to result in substantial loss in yield.

The importance of destroying hibernating larvae of the pink bollworm, *Pectinophora gossypiella* (Saunders), by cutting and burning cotton plants soon after harvest, along with fall plowing to reduce the populations, has been recognized for many years. Community-wide stalk-shredding, followed by plowing-under of the shredded material, is now considered the most important measure in the control of the pink bollworm. If the best stalk-shredding equipment is used, a large percentage of the population can be destroyed by a routine farm operation. Also, the plowing-under of infested material to a depth of 6 inches will greatly reduce the fall populations. These two operations can reduce the late-fall populations of pink bollworms by 95% or more.

The reduction in overwintering populations of the European corn borer, *Ostrinia nubilalis* (Hübner), through the disposal of crop residue was advocated in Europe as early as 1897. Similar practices have been used in the United States. The effectiveness of these practices depends on unfavorable ecological conditions for development of the borer the following spring. The most effective reductions of the overwintering population can be obtained by ensiling, by shredding or husking machines, and by plowing-under the crop residue to leave as clean a surface as possible. Research and practical experience by many workers in different countries show varying control, from none to a high degree, for the sugarcane borer, *Diatraea saccharalis* (Fabricius), and other species when infested central buds of cane are cut out in the early growing season and either burned or fed to domestic animals. Variable results may be attributable to the different species of borers studied; a variation in efficiency of treatment, overlap of generations, and other unidentified factors. Large numbers of overwintering sugarcane borers may be killed by plowing-under shaved stubs and millable residues of sugarcane, *Saccharum officinarum* L. (Figures 18 and 19).

Destruction of tobacco stalks after harvest reduces the number of late-instar tobacco hornworms, *Manduca sexta* (Johannson), tobacco budworms, *Heliothis*

FIGURE 18 **Millable sugarcane and high stubs left in fields after harvest in Louisiana. Large numbers of sugarcane borers overwinter in these materials. (USDA photograph)**

virescens (Fabricius), and corn earworms, *Heliothis zea* (Boddie), and results in fewer moths to infest tobacco, *Nicotiana tabacum* L., the next growing season. The destruction of vines and infested potatoes are important practices in the control of the sweet potato weevil, *Cylas formicarius elegantulus* (Summers), and the potato tuberworm, *Phthorimaea operculella* (Zeller).

Decaying and dropped fruit harbor important insects, such as the plum curculio *Conotrachelus nenuphar* (Herbst), codling moth, *Carpocapsa pomonella* (Linnaeus), and apple maggot, *Rhagoletis pomonella* (Walsh), and should be destroyed. Frequent collections of fruit are necessary; the fruit should be fed to livestock or made into cider if the quality is good enough. Many vegetables left in the field or around packing sheds harbor insects, as, for example, cabbage and other cole crops infested with caterpillars. These should be fed to livestock or destroyed.

Trees

Several species of destructive bark beetles are attracted to slash following logging operations. Removal or destruction of this material reduces the amount

FIGURE 19 **Shaved stubs and millable sugarcane residues plowed-under in Louisiana. Large numbers of overwintering sugarcane borers are killed by this practice. (USDA photograph)**

of breeding and prevents outbreaks from developing and killing living trees in the vicinity. Techniques of slash disposal have been developed for use against several species in pine stands in the South and West. Burning of elm logs and branches infested by the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham), and the native elm bark beetle, *Hylurgopinus rufipes* (Eichhoff), is a highly recommended practice in control of these vectors of the fungus causing Dutch elm disease, *Ceratocystis ulmi* (Buisman) C. Moreau.

Trees or branches heavily encrusted with scale insects should be destroyed as a protection against infestation in nearby trees. Also, abandoned orchards or neglected fruit trees should be destroyed; otherwise they will serve as breeding sources of many insect pests that will migrate to useful orchards. A high degree of control of a variety of twig girdlers affecting fruit, nut, and shade trees can be obtained by gathering and burning the severed branches late in the fall, or in the winter or early spring, when the eggs and grubs are in the twigs.

Pasture

The pasturing of livestock on remnants of crops as a means of controlling insects is an old practice that can be used provided objectionable insecticidal residues are not present. The utility of the method depends on the insect involved, timing of the operation, and thoroughness of the cleanup. Infestations of European corn borers may be reduced as much as 21% in heavily pastured and tramped fields of corn. Heavy pasturage of cotton fields by goats or cattle may provide better than 94% kill of pink bollworms.

CLEAN FIELD BORDERS

Many crop insects can feed and reproduce on weeds growing in field borders and later infest adjoining crops. Weeds, boards, boxes, sacks, dead vegetation, or dense grass in field borders may furnish ideal hibernating quarters for insects that will attack crops the next season. Wild host plants in field borders frequently harbor plant-disease organisms or their insect vectors, or both. Therefore, cleaning field borders is usually a desirable cultural control practice. However, field borders may also harbor beneficial insects, such as native bees, which are useful as pollinators, and parasites and predators that aid in insect control. Field borders also provide a desirable wildlife habitat. Trash and dense grass can often be removed without burning or plowing the field borders. A study of the insects and wildlife inhabiting borders of fields in specific areas should indicate the advisability and extent of cleanup that would be useful.

Clean field borders enhance control of the sorghum midge, *Contarinia sorghicola* (Coquillett). In the United States, sorghums, *Sorghum vulgare* Pers., sudangrass, *Sorghum sudanense* (Piper) Stapf., and broomcorn, *Sorghum technicum* (Koern.), are often severely damaged by this pest. The most important source of infestation is johnsongrass, *Sorghum halepense* (L.) Pers., in or along the borders of the fields, which serves as host and hibernation quarters for the midge. Before the sorghum comes into bloom, the johnsongrass permits the development of one or two generations of the midge.

Several vegetable insects, such as the squash bug, *Anasa tristis* (DeGeer), and the harlequin bug, *Murgantia histrionica* (Hahn), often hibernate in trashy field margins. The green peach aphid, *Myzus persicae* (Sulzer), an important vector of the "yellows" virus on sugarbeets, *Beta vulgaris* L., sometimes overwinters in the apterous form in weeds growing in or near drainage ditches. These weeds may also be an overwintering source of the virus. The control of weeds in drainage ditches by flaming or other methods reduces overwintering aphids and thus decreases the incidence of "yellows" in nearby beet fields.

The Japanese beetle, *Popillia japonica* Newman, is attracted to weeds such as elder, *Sambucus canadensis* L., smartweed, *Polygonum* spp., and wild summer grape (Vitaceae). These plants in and around a field or orchard are suitable food plants and may serve as a continuous source of infestation that should be destroyed.

DISPOSAL OF WASTES

Adequate disposal of wastes is the most important means of controlling many insects, particularly the house fly, *Musca domestica* Linnaeus, and the stable fly, *Stomoxys calcitrans* (Linnaeus). Disposal is often effective when used alone, but supplemental controls may sometimes be necessary.

House flies must have access to moist organic matter in order to reproduce. Proper disposal of wastes blocks such access. Scattering manure on agricultural land to dry before fly larvae have time to complete development has long been practiced and is an effective cultural control method.

Where low-value land is available or where land levels need to be raised, sanitary landfills are useful for the disposal of organic debris. In this procedure the wastes are thoroughly compacted, covered with earth, and again compacted to deny access of most insects to the organic material.

Composting of organic matter provides adequate disposal, produces useful fertilizers, and, if carefully controlled, prevents most fly-breeding. Some municipalities burn wastes, but others are developing modified composting units that reduce their garbage to useful products by mechanical and microbial means. The organic material is ground and placed in large rotating cylinders into which oxygen is introduced to encourage microbial action. In about 10 days the garbage has been converted into a commercially desirable fertilizer that is free of pathogens and odors, is of desirable consistency for application as fertilizer, and is high in needed plant nutrients.

Sanitation around mushroom houses is important in the control of flies and other pests on this crop. This involves removal of old compost and destruction of all plant residues as soon as they are removed from the house.

Food-processing plants must have adequate facilities for collecting and storing or disposing of organic wastes to avoid problems with Drosophila flies and other insects. The garbage should be disposed of at least daily, after which containers and equipment should be cleaned.

IMPROVED STORAGE AND PROCESSING

Storage structures must be well built and properly designed for commodities such as grain, seed, and fiber, for finished food and feed products, and for fabrics. Keeping the storage facility and the commodity as cool and dry as possible reduces the insect-infestation hazard. Artificial drying of moist grain before storage and forced-air cooling in storage bins are measures that help hold down insect populations. Several of the better standard warehousing practices are helpful in combating infestation in stored products. The old rule of "first in, first out" brings about a rotation of commodities to avoid unusually long storage, thus preventing the buildup of insect infestations that might spread to other products in the warehouse. Cleaning and inspection in the warehouse are facilitated by the arrangement and clearance of individual stacks.

Good housekeeping, with the emphasis on thorough cleaning, is essential in farm or commercial storage of grain and other raw food materials, as well as in mills, bakeries, food-processing plants, and food-handling or warehousing areas, to prevent infestations of stored-product insects. Bulk-storage bins, whether for grain, raw materials, or finished products, should be cleaned inside and out to be insect-free before filling. Any nearby sources of infestation should be eliminated. In grain elevators, there should be frequent cleaning and removal of waste grain, chaff, and grain dust from headhouses and tunnels, elevator boots and legs, dust collectors, and horizontal screw conveyors. Frequent use of heavy-duty industrial vacuum cleaners is an effective way of cleaning in grain elevators, mills, food plants, bakeries, and warehouses to keep insect populations at low levels. Broken or torn packages should be repaired or removed promptly from warehouse storage, and spillage should be cleaned up immediately.

Frequent, periodic inspections by trained personnel permit the detection of incipient infestations that may be eliminated before they spread or develop into damaging populations. Such inspections are applicable to mills, bakeries, and food-processing plants; to storage facilities for grain, seed, and other raw agricultural commodities; and for processed foods, feeds, and fabrics. Buildings should be inspected at least once a year for evidence of subterranean termite attack, so that infestations can be controlled while localized.

TILLAGE

Insects are greatly affected by the texture of soils, their chemical composition, the amount of soil moisture, the temperature, soil organisms, and by the effects of these factors on their food plants. Recognition has long been given to the principle of utilizing various methods of cultivating the soil to coincide with susceptible stages in the life histories of insects in order to control them. The application of soil tillage to control insects depends on a thorough knowledge of the insect's life history and habits. The nature and correct timing of the tillage should be compatible with good agronomic practices. Under some conditions tillage may favor certain pests, and under others it should be avoided at certain times.

Tillage during the time that crops are not growing on the land will destroy volunteer plants, stubble, and weeds that may provide food and a breeding site for certain insect pests that could infest newly planted crops. Cultivation may bury some insects so deeply that they cannot emerge, or it may bring insects that are in the soil to the surface, where they are devoured by birds or rodents or are killed by dry or cold weather.

Fall plowing results in high mortality of overwintering pupae of the corn earworm and thus reduces the number of adults that emerge the following spring. Deep plowing does not destroy all larvae of the European corn borer, but those that survive crawl to the surface and are easy prey to weather and natural enemies. Such plowing, preferably in the spring, should leave no stalk and weed fragments above the ground to provide refuge for the larvae. In North Dakota the emergence of the wheat stem sawfly, *Cephus cinctus* Norton, has been reduced by as much as 75% by cultivation of stubble.

Infestations of the grape berry moth, *Paralobesia viteana* (Clemens), on grapes have been greatly reduced by burying the overwintering cocoons under a layer of soil. The moths are unable to emerge and make their way to the surface in the spring (Figures 20 and 21).

FIGURE 20 Plowing-up of soil to and under the grape trellis as first cultural operation in the spring. Soil was too wet and thrown up in almost continuous slices which did not cover well around the vines and posts. Many openings were left for emergence of grape berry moths. Tillage should have been delayed until the heavy soil was slightly drier, so that it would break up more readily. (Photograph by G. W. Still, USDA)

FIGURE 21 Soil ridges thrown under grape trellis in the spring. Under trellis covered well, considering that tractor could not go too close to vines because of crooked vines. Low, smooth, compact ridge is desirable to prevent emergence of grape berry moth. (Photograph by G. W. Still, USDA)

Tillage can destroy many grasshopper eggs. Grasshopper-infested grain stubble to be summer-fallowed should be worked in the spring before eggs hatch. Plowing is more effective than disking or other methods of cultivation, but, where wind erosion is a problem, plowing is not recommended. Grasshoppers will not lay eggs in summer-fallowed land cultivated in the fall.

Cultivating may sometimes destroy all vegetation, and insects may starve. For example, in Kansas, grasshopper infestations did not develop in wheat-stubble fields having many egg pods of the migratory grasshopper, *Melanoplus sanguinipes* (Fabricius), when the soil was worked one to three times before and during the hatching period, and all green food was destroyed by intense cultivation.

In Canada, clean summer fallowing every second or third year to eliminate living plants that serve as food for wireworms (Elateridae) will reduce larval populations to levels where they will cause little damage. Two or three fallows may be necessary to reduce a severe infestation as effectively as one chemical seed treatment. Fallowing will also prevent an increase in populations where most of the wireworms have been killed by chemical seed treatments.

The destruction of volunteer wheat is an important control measure for the wheat curl mite, *Aceria tulipae* (Keifer), the vector of the virus causing wheat streak mosaic. Neither the vector nor the virus is able to live over the summer in stubble or dead plants. Summer tillage of land to be planted to winter wheat will eliminate host plants and the mite vector.

Effective cultural control practices may sometimes be based on a knowledge of when not to till the soil. For example, in Canada, best control for the pale western cutworm, *Agrotis orthogonia* Morrison, and some other cutworms is to allow summer-fallowed fields to become crusted in August and September. The female moth will not lay eggs on crusted soil. Cultivating summer-fallowed land should be delayed until the end of July and, if necessary, resumed in October.

Past successes in using various tillage methods for control of a wide range of insects certainly suggest that much more research should be directed to this type of control in consonance with good agricultural practices. The key principle to the use of cultivation for insect control lies in timing the operation to take advantage of the weak link in the life cycle of the pest. Since species differ greatly in habits, each one must be considered individually. The degree of insect control might be greatly increased if a satisfactory practice could be carried out over the entire distributional area of the infested crop.

ROTATIONS

Much has been learned about preventing insects from becoming seriously destructive in cultivated fields by following the principle of a good rotation in which a crop of one plant family is followed by one from a different family that is not a host crop of the insect to be controlled. Agronomic research and practice have shown that some rotations that are advantageous from the viewpoint of insect control may be harmful for other reasons; for example, rotation from sod crops on hilly land may lead to soil erosion. The advantage of agronomic developments such as growing corn continuously without crop rotations must be weighed against increased infestations of root-infesting insects and nematodes. Crop rotation is most effective against insects with a restricted host range and those having limited powers of migration.

CROP ROTATION

White grubs feed on roots of many crops. However, some leguminous crops are unfavorable to their development. The proper use of legumes in rotation with grass crops greatly reduces white grub injuries. Excellent control of white-fringed beetles, *Graphognathus* spp., is possible by following certain rotation practices. These beetles, which cannot fly, will lay many eggs when the adult feeds on peanuts, *Arachis hypogaea* L., soybeans, *Glycine max* (L.), and velvetbeans, *Mucuna deeringianum* (Bort). The grasses, including corn, *Zea mays* L., and small grains, are poor foods, and adults feeding on them lay few eggs. Grasses do not suffer as heavy damage by larvae as do plants having taproots. A knowledge of these factors has made it possible to keep the population low by following certain cropping practices. Legumes should never follow legumes in the cropping rotation for controlling this pest.

Studies on crop rotation in Idaho and Washington showed that certain wireworm populations increase immediately following the growing of red clover, *Trifolium pratense* L., and sweetclover, *Melilotus* Mill., but decrease with each succeeding year of alfalfa, *Medicago sativa* L., probably because alfalfa takes moisture from a greater depth than do the clovers. Potatoes, *Solanum tuberosum* L., being very susceptible to wireworms, are best grown immediately following alfalfa. In the northeastern and north central United States, a short crop rotation is used even if the wireworm population is low enough to permit growing of potatoes. The alternate green-manure crops that are resistant to wireworms include crimson clover, *Trifolium incarnatum* L., and buckwheat, *Fagopyrum esculentum* Moench.

Crop rotation is often an effective control for insects that lay their eggs in fields that have not yet been planted. Eggs of the northern, *Diabrotica longicornis* (Say) and western, *Diabrotica virgifera* LeConte, corn rootworms are laid primarily in cornfields in the fall; the larvae feed primarily on corn roots and cannot migrate to other fields. A rotation with not more than two successive crops of corn has been recommended. However, a 3-year rotation, 2 years of corn and 1 of oats, will not give complete control, because some eggs will be laid in oat-stubble ground.

Several mites that attack field crops can be effectively controlled by crop rotation. The winter grain mite, *Penthaleus major* (Dugès), which is a serious pest of wheat, *Triticum aestivum* (L.), oats, *Avena* L., and barley, *Hordeum vulgare* L., can be effectively controlled by not planting small grains more than 2 years in succession in the same field.

ANIMAL ROTATION

The elimination of bovine piroplasmosis, *Babesia bigemina* (Smith & Kilbourne), from the United States by eradicating the cattle tick, *Boophilus annulatus* (Say), was greatly aided by pasture rotation. Keeping the pastures completely free of bovine animals resulted in the starvation of the ticks. During periods of high humidity and low temperatures, the ticks were able to live up to 10 months, but in hot dry weather the time needed for cleanup was greatly reduced. Ticks, such as the cattle tick, that depend primarily on a single animal species as a host and require blood meals at intervals of a few months may be successfully controlled, but ticks that can use many species of animals as hosts and live for long periods without feeding resist control by pasture rotation. In Oklahoma, pastures heavily infested with the lone star tick, *Amblyomma americanum* (Linnaeus), which parasitizes many species of animals, were kept free of cattle for 12 years, with a maximum tick reduction of 82%. When all animals except birds were eliminated from the pasture, the numbers of lone star ticks present dropped to 2% of those found in the control areas.

Removal of animals from lowland to upland pastures often greatly reduces injury by tabanid flies (horse flies and deer flies). Tabanid attack in many parts of the western United States is localized in the vicinity of tree belts or small streams. Utilization of these pastures in spring and early summer, and the pastures that have very few trees during the late summer and fall when the tabanids are active, is considered a part of good livestock management in the western part of Oklahoma and Kansas.

LAND, LIVESTOCK, AND TREE MANAGEMENT

Some land utilization and management practices that influence insect populations were considered in the sections on tillage and rotations. Other procedures, such as temporarily removing land from cropping and diverting it to soil-building plants, and strip-cropping, may also alter insect populations. Planting dates can often be adjusted to prevent synchronization of the insect with the crop. Other management practices, such as the use of clean seed, choice of method of planting, location of the crop in relation to other crops or previous crops, destruction of alternate hosts, elimination of early blooms, choice of fertilizer, spacing of crops, and a variety of harvesting procedures, may influence the amount of insect damage. Livestock-management practices such as time of calving, dehorning, and castration can be regulated to prevent damage by insects. However, much research remains to be done to exploit these management procedures to the fullest as acceptable ways to control insects.

LANDBANK

The landbank or soilbank programs in the United States involve acreages set aside to avoid additional production of surplus agricultural crops. Such land is usually seeded to legumes for soil improvement, left fallow except for the requirement of destroying weeds, or converted to wildlife refuges or forests.

Such major changes in land use undoubtedly will greatly influence insect populations, but studies of these changes in relation to insect control are lacking.

STRIP-CROPPING

In the northwestern Great Plains of the United States and Canada, the practice of strip-cropping to prevent wind erosion of the soil and to retain snow for water conservation has provided ideal conditions for the wheat stem sawfly. A narrow strip of wheat alternates with a strip of fallow, and the sawfly migrates from stubble (fallow) to the nearby growing plants. Strip-planting of wheat, as often practiced in western Kansas, increases the damage caused by the migratory grasshopper in fall-planted wheat. The damage is more extensive when the wheat borders small grain stubble than when it borders sorghums. Strips can be arranged and rotations can be made within strips so that wheat is not bordered by wheat stubble. In California, strip-farming of alfalfa assists in the biological control of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton). When each set of alternate strips is cut, the other strips are about one half grown, and the field is never bare of the growing host hay. This provides for a better and more reliable population balance between the pest species and its natural enemies. Following the use of the insecticide demeton on strips of tall alfalfa, surviving beneficial insects migrate to the short alfalfa strips, rather than away from the field, and hold the aphid in check through the next cutting.

FERTILIZERS

Use of fertilizers to enhance plant nutrition often influences the longevity, fecundity, and damage of insects and mites. However, the idea that more vigorous plants or those growing in fertile soil are attacked less by insects is not always true. One review of the literature on the effect of soil elements on insect infestations cited 15 published references showing that high fertility or high amounts of nitrogen, phosphorus, or potassium in the soil increased insect injury or population and 14 that showed that insect injury or population was decreased under the same conditions. Thus, each species of insect, each species or variety of host plant, and each soil type seems to constitute a separate problem.

Chinch bugs, *Blissus leucopterus* (Say), prefer to congregate in the sun in the spring and seek out the thinner and poorer areas of small grain fields. A thick vigorous growth (such as from the use of fertilizer) and a heavy shade are unattractive to the insect. However, nitrogenous fertilizer caused an increase in damage to sorghum by chinch bugs. Phosphates encourage early development of wheat roots, and their addition to low-phosphorus soils has reduced wireworm damage. However, succulent rapid-growing corn is more attractive to the egg-laying European corn borer moth. Phosphorus applied alone or mixed with nitrogen at planting time was closely associated with an increase in the amount of cutting by the wheat stem sawfly in both winter and spring wheats. Potassium applied together with nitrogen and phosphorus tended to decrease the amount of sawfly-cutting in winter wheat, but nitrogen alone had little effect. In India, 100 lb or more of nitrogen per acre made sugarcanes soft, succulent, and subject to heavy injury by the borer *Chilotraea auricilla* (Dudgeon); higher levels of nitrogen increased stem-borer infestations by *Chilo partellus* (Swinhoe) and *Sesamia inferens* (Walker).

There also is little consistency in the results of fertilizer trials for forest-insect control. However, there appears to be general agreement that fertilization plays some part in reducing the populations of many forest-insect pests.

TIME OF PLANTING

Control of some insect pests is achieved by following the principle of growing the crop when the pest is not present or of planting so that the most susceptible stage of crop development coincides with the time of the year when the pest is least abundant.

In the United States, some insects, such as the corn earworm and fall armyworm, *Spodoptera frugiperda* (J. E. Smith), overwinter only in the south and gradually move northward during the growing season. Therefore, if corn can be planted early in the north, it may mature before these insects can migrate northward and become numerous. The sorghum midge can be effectively controlled in the Texas high plains if sorghums are planted early enough to bloom before the first week in August.

It is sometimes possible to avoid planting a crop before the time of egg-laying by an injurious insect. Adults of the Hessian fly, *Mayetiola destructor* (Say), normally emerge in the fall and live for only 3 or 4 days. If winter wheat is planted after most of this generation is past, the plants will have few eggs laid on them. Entomologists in the Hessian fly-infested areas of the United States have established dates for sowing winter wheat that will allow the plants to make satisfactory fall growth but be late enough to avoid heavy Hessian fly infestations. When Hessian fly-resistant varieties are not used, farmers should usually follow a safe seeding date.

In Russia, the late sowing of summer wheat brought about a decreased infestation on a flea beetle, *Chaetocnema hortensis* Geoff., and a thrips, *Haplothrips tritici* Kurd. In India, early sowings of wheat during the month of May were free from the attack of the gall moth, *Enarmonia pseudonectis* Meyr., but the sowings made in late June and early July were highly infested; however, early sowings were attacked by an agrotid caterpillar. In some areas, early plantings of sugarbeets may escape infestation by the beet leafhopper, *Circulifer tenellus* (Baker), the vector of the virus causing curly top disease, *Ruga verrucosans* Carsner and Bennett, while in other areas it is advisable to delay planting until after the spring leafhopper migration.

Early planting is an important factor in control of the southwestern corn borer, *Zeadiatraea grandiosella* (Dyar). Lower infestation and consequent higher yield of the early corn-plantings result when moths of the late broods deposit fewer eggs on the mature plants. In areas where the European corn borer has only one generation a year, early-planted corn has a higher infestation than late-planted corn. Where two generations occur, late plantings will probably be injured more by the second brood. For centuries, Chinese peasants have used the proper selection of grain-sowing dates to prevent damage by the rice borer, *Schoenobius incertellus* (Walker), the wheat stem maggot, *Meromyza americana* (Fitch), and a pest of millet, *Chilotraea infescatellus* (Smell).

Choice of the proper planting date for young pines in areas where pine stands have been removed by cutting or fire is an effective means for preventing damage to the young pines by the pales weevil, *Hylobius pales* (Herbst), and the pine root collar weevil, *Hylobius radicis* Buchanan. In the southern areas of the United States a waiting period of 9 months is sufficient, but in the northeastern areas the waiting period should be extended to 2 to 3 years.

INSECT-FREE SEED AND SEEDING METHODS

The use of insect-free seed is a sound principle for insect control on some crops. Some species of insects remain within the seed from harvest to planting time. The bean weevil, *Acanthoscelides obtectus* (Say), breeds and increases in dry stored seed. If infested seed is planted, the adults will emerge from the seed and infest the growing crop. Potatoes infested with the potato tuberworm should not be used for seed. To reduce losses from the alfalfa seed chalcid, *Bruchophagus roddi* Gussakovskii, all farmers in a locality should grow seed from the same cutting. When first- and second-crop seed are grown in the same locality, the first crop serves as a source of infestation for the second, thus increasing losses.

The rate and depth of planting or the availability of soil moisture for rapid germination may influence insect damage. Since the larvae of the false wireworms (Tenebrionidae) are especially injurious to seed before it germinates, any measure that hastens germination, such as planting in a well-prepared seedbed when there is sufficient moisture, aids in reducing damage. Shallow seeding of wheat reduces damage by some species of wireworms because the warmer and drier conditions near the surface are less attractive to them. Several workers have recommended the seeding of a few extra pounds of wheat in soil infested with wireworms, since the numbers of head-bearing stems developed are about the same in thick as in thin stands. Infestation and cutting by the wheat stem sawfly decreased as seeding density increased and row-spacing decreased. Sawflies apparently select the larger, more succulent stems in the thinner stands for oviposition.

DESTRUCTION OF VOLUNTEER PLANTS

Volunteer plants are very attractive to many insects and serve as the focal point for future infestations. There is a practical value in destroying volunteer plants to curtail infestations of grasshoppers, Hessian fly, sweetpotato weevil, potato tuberworm, potato aphids, *Macrosiphum euphorbiae* (Thomas), and wheat curl mite. Hail and changing agricultural practices have sometimes contributed to the population of volunteer plants. When wheat is combined much grain is left in the field; this comes up in the summer and is ideal for development of a late-summer brood of the Hessian fly. A cleanup program to plow under the stubble may be impossible when the land is seeded to clovers and grasses to provide pasturing and soil improvement, or where the soil is likely to blow.

DESTRUCTION OF ALTERNATE HOSTS

Many insects reproduce on weeds or other alternate hosts and then attack the main crops. It is therefore usually desirable to destroy brambles or other weeds on uncultivated land to assist in the control of insects such as aphids, beet leafhopper, raspberry caneborer, *Oberea bimaculata* (Olivier), Japanese beetle, sweetpotato weevil, and sorghum midge.

REPLACEMENT OF FAVORED OR ALTERNATE HOSTS

Progress toward the control of the beet leafhopper by substitution of grasses for broadleaf annual plants in its breeding area of southeast Idaho is an outstanding example of how the principle of replacement of favored hosts can be used for insect control. The beet leafhopper is the sole known vector of the virus of curly top, a serious disease of several crops in southern Idaho. The insect breeds and maintains itself on Russian-thistle, *Salsola tenuifolia* Tausch, in large desert and range areas, a major portion of which is public domain. Since

1959, more than 116,000 acres of this leafhopper-breeding area have been seeded to suitable perennial range grasses, primarily crested wheatgrass, *Agropyron desertorum* (Fisch.) Schult. This host replacement has resulted in a marked decrease in the movement of the beet leafhopper into cultivated areas and in a substantial reduction in curly top disease in beans.

In the northern Great Plains, replacement of broad-leaved weeds along roadsides and fencerows with perennial grasses greatly reduces the number of grasshoppers in these locations. Native or prairie grass attracts few migratory grasshoppers, but if too much time is required for it to become established in a regrassing program, the desirable crested wheatgrass can be used. Additional detailed information on food habits of grasshopper species now being acquired should make more intelligent use of alternate plants possible.

DISTANCE FROM OTHER PLANTINGS

The infestation and damage to a crop by an insect pest can sometimes be reduced by planting one crop as far away as possible from another crop that is known to become infested earlier in the season. However, because of costs, it is seldom practical to utilize this method of control. The first generation of chinch bugs, for example, breeds in small grains and migrates by crawling to corn and sorghum when the small grains mature. Damage to corn can be reduced by planting it a considerable distance from small grains. Another example is the wheat straw-worm, *Harmolita grandis* (Riley), which feeds only on wheat and is wingless in the spring form. It is controlled if winter wheat is seeded 60 yards away from the previous crop.

The larval stage of one insect may feed on one crop and the adult on another; therefore, separating the two crops may aid in control. Cotton and soybeans should not be planted next to wheat heavily infested with the southern masked chafer, *Cyclocephala immaculata* (Olivier), since the adults emerging from the wheatfield will feed on the leaves of the other plants. In the control of the potato tuberworm, it is important to separate the late-planted from the early-planted crop. To avoid curly top infection in root beds, sugarbeet seedlings should be grown in localities where they are not exposed to beet leafhoppers.

DESTRUCTION OF EARLY BLOOMS

The control of some insects can be helped by the destruction of blooms prior to bloom of the main crop. For control of the sorghum midge, sorghum heads cut within 5 days after the first blooms appear can be left on the ground, where the midges will die. If cut later, especially in the fall, they should be removed from the field before the midges can emerge from them.

CROP-SPACING

Spacing may affect the relative rate of growth of a plant and its pest population per unit of time and the behavior of the insect pest in searching for food or an oviposition site. Close spacing of plants may add to the effectiveness of natural enemies and result in greater control of pest populations. The weevil *Thylacites incanus* (Linnaeus), is an example of a pest adversely affected by crop-spacing. It can develop only while the foliage of spruce trees has not formed a closed canopy. The eggs of this beetle, which are laid on the ground, probably get sufficient heat for development only when the sun's rays can reach the ground; therefore, it appears that the pest can be controlled by causing a young plantation to form a closed canopy as soon as possible.

TIME OF CALVING, DEHORNING, AND CASTRATION

In areas where screw-worm flies, *Cochliomyia hominivorax* (Coquerel), occur, proper care of livestock demands that any management practice that may result in an open wound should be done during the coolest period of the year, when the screw-worm flies are absent or scarce. Even in areas of the United States where the screw-worm has been eliminated, dehorning, castrating, and calving should be scheduled to avoid the active period of other myiasis-producing flies. House flies and related species often frequent wounds and transfer microorganisms; therefore, most ranchers avoid dehorning and castrating in the summer, even when screw-worms are not a problem.

HARVESTING PROCEDURES

Harvesting procedures involving the proper state of crop maturity, timing the harvesting or cutting practices, and strip-harvesting offer considerable assistance in the control of a variety of insects. As additional detailed biological studies of pests are made, it is likely that greater use can be made of harvesting methods in insect control, either alone or in concert with other methods. One severe handicap has been lack of definitive measurements of the effects of selected harvesting procedures against pests in an isolated area involving the total insect population.

State of Harvesting

The harvesting of crops as soon as they attain the right stage of maturity is usually accompanied by many side advantages in addition to the important ones of increased yield and curtailment of insect damage to the current and future crops. Sweetpotatoes, *Ipomaea batatas* (L.), and Irish potatoes should be harvested as soon as they are mature, to reduce damage by the sweetpotato weevil and the potato tuberworm, respectively. Peas should be picked as soon as they ripen, to avoid pea weevil, *Bruchus pisorum* (Linnaeus), damage. Cabbage, *Brassica oleracea* var. *Capitata* L., should be cut when mature, to reduce damage by lepidopterous caterpillars, *Pieris* spp., and the cabbage looper, *Trichoplusia ni* (Hübner). Fields heavily infested with the sugarcane borer should be harvested as early as possible, to minimize losses.

Selective cutting is an effective method of reducing losses caused by certain forest insects. Its use and effectiveness depend on the detection of those trees in a stand that are most likely to be attacked. This system has been particularly successful in control of the western pine beetle, *Dendroctonus brevicomis* LeConte, in ponderosa pines in parts of the western United States (Figure 22).

Time of Harvesting

Time of harvesting may have a pronounced effect on the insect population of a field. In a crop such as alfalfa, which is cut several times a year, harvesting suddenly changes the physical environment of the field, and it generally becomes much hotter and drier. Such changes in the environment cause insects to leave, seek shelter, or die. As regrowth of the crop takes place, movements of the insects into or out of a field occur, direction of movement depending on preferences of the pest for various conditions of the host plant. Damage to alfalfa by the potato leafhopper, *Empoasca fabae* (Harris), could be reduced in most years in Wisconsin by harvesting the second alfalfa cutting at the very-early-bloom or late-bud stage. Early cutting of the first and second crops of alfalfa is a practical control method for the alfalfa weevil, *Hypera postica* (Gyllenhal).

The late-season or fall behavior of adults of the meadow spittlebug, *Philaenus spumarius* (Linnaeus), determines the location and extent of the next year's nymphal populations, and the time of cutting the meadow determines the attractiveness or unattractiveness of legume fields as feeding sites. The adult spittlebug tends to settle on plants that provide suitable succulent foliage for feeding. Spittlebugs deposit most of their eggs in the fall of the year. New seedings of alfalfa, which in the spittlebug area are usually planted in grain crops in the spring, are in a very succulent condition after late summer clipping; adults therefore deposit large numbers of eggs in these first-year alfalfa meadows, and heavy infestations of nymphs occur in such fields the following

FIGURE 22 A mobile loader used in the sanitation-salvage logging of ponderosa pine to reduce losses caused by the western pine beetle. Infested trees and those considered most likely to be killed by the beetle in the near future are removed to reduce the beetle population and to improve the condition of the residual stand. Lassen National Forest (U.S.A.) (USDA photograph)

spring. Older stands of alfalfa in Ohio are managed on either a two-or three-cutting schedule. In the two-cutting fields, if the second cutting is harvested in early August, attractive succulent foliage is available in September for spittlebug oviposition; if it is harvested in July, the plants will be more mature in September and not so attractive for oviposition. Under the three-cutting schedule the last cutting is removed in early September, and no succulent growth is available for oviposition.

A crop can sometimes be harvested before maximum insect damage occurs. The wheat stem sawfly causes considerable damage by tunneling the stem, and complete loss may occur if harvesting of infested wheat is delayed until the plants lodge or bend over because of larval cutting. In the infested area of South Dakota, the practice of cutting wheat early, and threshing from the windrow by using a pickup attachment on the combine reduces the grain losses caused by the sawfly. Present methods of harvesting corn with a high moisture content may allow corn to be harvested before "ear drop" caused by European corn borer damage. Growers of cotton endeavor to mature a crop before a population build-up of the boll weevil can do extensive damage.

Timber cut during certain parts of the year is much less susceptible to damage by many species of insects than when cut during other seasons. Logs cut from late summer to early winter are least likely to be damaged by boring insects; within this range, the period of least susceptibility depends on locality. Losses caused by many species of bark beetles, *Ips* spp., in pine stands following cutting or logging operations can be prevented or materially reduced by proper planning and execution of these activities. Small-scale cuttings, which are usually completed rather quickly, are relatively safe when made only during the fall and winter months. Large-scale cuttings, many of which take considerably longer, are also relatively safe, provided they are not discontinued or completed during the summer months.

Strip-Harvesting

Strip-harvesting of alfalfa may reduce lygus bug infestations in adjoining crops. Under this system, alfalfa is harvested in alternate strips, so that two different-aged hay growths occur simultaneously in a field. When one series of strips is cut, the alternate strips are about half grown. The field becomes a rather stable environment, and lygus bugs (*Lygus* spp.) move into the younger hay strip as the older strip is harvested, instead of flying to adjoining crops as they do if the entire field is cut at one time. Since natural enemies of the lygus also move from strip to strip, there is no increase in lygus populations. When the lygus adults move into the uncut strip, they deposit eggs in the half-grown hay, but, since the hay is cut in about 15 days, many of the eggs and newly hatched nymphs are removed or destroyed at harvest.

Time of Shearing

Wool maggots (Calliphoridae) may create a serious problem in sheep during periods of continued humid weather. Merino and Corriedale sheep are most susceptible to wool maggot attack, but all breeds may be affected. Moist parts of sheep are the most attractive oviposition sites for the flies.

Removal of the fleece at the onset of long-continued humid weather provides excellent control, but this practice may not be consistent with good management. In this case, selective shearing of parts of the sheep most susceptible to attack, such as the escutcheon and back of the hind legs of females or the prepuce of males, provides a high degree of protection.

OTHER PRACTICES

The management of bermudagrass, *Cynodon dactylon* (L.) Pers., pasture is important in control of the spittlebug, *Prosapia bicincta* (Say). Heaviest infestations are always found in the rank uncut area or in an ungrazed area. Burning the refuse and dead grass in the fall is also an effective control method. In areas where grasshoppers could be pests, a sound control method is to avoid uncultivated dividers between fields; they provide favorable areas for grasshopper egg-laying.

TRAP CROPS AND LOGS

Trap crops and trap logs have been tested for many years, with some success but with many failures, as methods of insect control. The limitations were partly attributable to insufficient trapping material to attract and absorb enough of the insect population to provide substantial control. The method has proved inefficient and too costly for control of most insects.

A trap crop is a small planting, often made earlier than the main planting, to attract insects or divert them away from the principal crop. The trap crop must usually be destroyed before the insects can reproduce. The crop used must be very attractive to the insect.

Trap crops may be used to attract insects at an early stage, encourage reproduction of parasites and predators, and thus bring about better biological control. Biological control of the citrus red mite, *Panonychus citri* (McGregor), has been augmented by planting permanent pasture grasses as cover crops. These grasses provide favorable environmental conditions for the development and multiplication of the predators of the host mites. They also favorably modify the physical environment through decreased radiation, increased humidity, and dust control.

Certain species of bark beetles are more strongly attracted to recently cut logs than to living trees while flying in search of food or mates, and such logs can be used as traps in the control of a few species. This method of control has been used effectively against the Engelmann spruce beetle, *Dendroctonus obesus* (Mannerheim), in the Rocky Mountain region of the United States.

REGULATION OF PLANT STANDS

The interplanting of agricultural crops, mixtures of crops and weeds, regulation of the stand composition of forests, or even the selection of one sex of a shade tree, may have a considerable bearing on reducing the size of an insect population and the severity of damage.

Cover crops in citrus groves in Florida affected the population of injurious citrus insects and mites. Six major pests studied were reduced in numbers or partly controlled by reducing cover-crop cultivation to a minimum consistent with efficient grove management. Two other species may have become more abundant under the same conditions. Mixed stands of weeds intermingled with a crop may influence insect populations. Alfalfa alone is an unsatisfactory diet for several grasshoppers, but alfalfa supplemented by some of the weeds commonly found in alfalfa fields furnishes an adequate diet. Thus, 3- to 5-year-old stands of alfalfa, which are often weedy, usually have more grasshoppers than 1- or 2-year-old stands.

Forest management involves the treatment of stand factors to maximize growth or other desirable phenomena. The rationales for silvicultural control of insects lie in the concept that since species composition and stand structure are being manipulated for other purposes, information relating to insect epidemiology should also be incorporated into silvicultural systems to yield maximum resistance to pests. When a large enough fund of ecological information is available to allow an understanding of basic mechanisms involved in natural systems, the principles can be built into the synthetic management schemes at almost no cost.

Regulation of stand compositions offers opportunities for preventing or reducing the frequency and intensity of outbreaks of several important forest insect pests. The success of insect control after logging, by modification of the composition of the stand, depends on the establishment of an adequate amount of reproduction of all the desired species needed in the future stand. In single-species forests, regulation is secured by either scattered cutting or plantings. In mixed stands containing a high proportion of susceptible species desirable change is secured by selective cuttings to reduce the proportion of susceptible trees in the final mixture. There is considerable evidence that the boxelder bug, *Leptocoris trivittatus* (Say), a nuisance in homes, can be largely eliminated by limiting shade-tree plantings of boxelder to staminate trees.

SELECTION OF SITE

Silvicultural control practices based on a consideration of site conditions are recommended for control of several important forest insects. Utilization of white-birch forests growing on poor sites, before they begin to deteriorate, or the conversion of temporary birch forests growing on such sites to other species better suited to the sites, is recommended for control of the bronze birch borer, *Agrilus anxius* Gory. Healthy, vigorous trees are not usually seriously damaged by this species. Selection of the proper site for planting many species of trees is recommended for the prevention of future losses by certain insects. Black locust trees planted on good sites are much less subject to future damage by the locust borer, *Megacyllene robiniae* (Forster), than if planted on poor, slow-growing sites. Damage caused to jack pine and Scotch pine by the pine root collar weevil, *Hylobius radicis* Buchanan, in the Lake States of the United States is most severe in trees growing on sandy, well-drained soils. To reduce future losses, it is recommended that such areas be avoided in planting these species.

THINNING AND TOPPING

Thinning and "topping" are practices that influence insect populations, and the timing of these operations can be utilized to advantage in the control of some species.

The topping of tobacco affects populations of the tobacco hornworm, the tobacco budworm, and the corn earworm. Shortly after flowering, tobacco plants are usually "topped," i.e.,the terminal portion of the plant, including floral structures, is removed. Topped plants or cut stalks (after harvest) produce sucker growth. Suckers are usually removed by hand or prevented from developing by a chemical growth inhibitor. Where the growth inhibitor is used or stalks are cut, populations of the three species are consistently lower. The highest populations of hornworms and budworms are found on plants topped and manually suckered. Earworm populations are heaviest on untopped plants. Thinning of cabbage and other cole-crop transplants to a nearly perfect stand of sound terminal buds is advised. Moderate insect injury by lepidopterous caterpillars to the terminal bud often disfigures the plant, and severe injury may stop growth of the bud.

Removal of part of young dense stands of trees by thinning is often useful in improving the vigor of the remaining trees and in reducing the development of destructive insect infestations. This is especially true in stands occupying dry sites.

PRUNING AND DEFOLIATING

Pruning of both young and mature trees and the destruction of insect-infested materials are worthwhile principles to follow in preventing insect damage to forest, fruit, and shade trees, as well as ornamentals and some other plants. It is recommended as a method of control of the European pine shoot moth, *Rhyacionia buoliana* (Schiffermüller), in pine plantations in the Lake States of the United States and of bark beetle vectors of the fungus-producing Dutch elm disease. As a control method, pruning is most applicable to the care and protection of fruit and high-value shade and ornamental trees.

Purposeful defoliation may affect the control of mites. A red spider, *Oligonychus coffeae* (Nietner), a pest of tea, *Thea sinensis* L., in India persists on a few old leaves and on the scale leaves at the base of the shoots during cold weather, and this small population is primarily responsible for the attack the next spring. The mites are removed by stripping these infested leaves. In the United States defoliants and desiccants are used on cotton to reduce the fall population of the pink bollworm.

WATER MANAGEMENT

The management of water can favor or hinder the development of insects. Procedures have been developed to regulate water use, and, when timed with a critical stage of the life history of some insects, a remarkable degree of control can be obtained. Insects of agricultural importance and those of great nuisance to man and animals can be controlled by the careful application of water-management procedures. Many important advancements have been made in this field, and biologically sound recommendations are being followed by various soil- and water-management agencies. However, the great diversity of insect species and the infinite variety of aquatic habitats clearly show the need for additional biological and control work.

Water-resource projects, especially impoundments and irrigation developments, may create a number of undesirable insect problems. However, many natural aquatic or semiaquatic environments, including saltwater and freshwater marshes, swamps, and depressions, are favorable for the production of mosquitoes (Culicidae), horse flies and deer flies (Tabanidae), and biting midges (Ceratopogonidae), which are serious pests of man and animals. Increase in population of these pests can be minimized and in some cases prevented by proper planning and construction, alterations of the natural breeding sites, and appropriate water-management procedures. Basic guidelines for such procedures have been fairly well established. However, they need to be adapted to specific problem areas and to be modified and refined to keep pace with advances in control concepts and for better integration of insect-control techniques with other interests such as fish and wildlife, water storage, flood control, power production, and recreation.

IRRIGATION

Crop Infestations

Moisture is an important limiting factor in the ability of some wireworms (Elateridae) to survive in soils. Flooding of infested soils in the northwestern part of the United States eliminates the wireworms in 3 days but is not practical, because the water leaches out alkali salts that adversely affect subsequent crops. Other wireworm species are unable to withstand desiccation.

Where they occur, drying out the soil is an effective control measure. Crops such as fall grains and alfalfa should receive a minimum of irrigation water the year before the field is to be planted to truck crops.

Where sufficient water is available, flooding is sometimes used for insect control. Flooding of sugarcane fields to drown borers in the planted seedcane and in cane trash has been practiced in some countries. Sugarcane borer infestation in Louisiana was reduced by flooding but increased rapidly the second year after inundation. Flooding sometimes injures the cane stubble and soil. In India, heavy infestations of *Chilotraea auricilia* (Dudgeon) were observed after the fields had been waterlogged. Flooding hay meadows where eggs of the clear-winged grasshopper, *Camnula pellucida* (Scudder), have recently hatched will destroy many of the young grasshoppers. Flooding rice paddies for at least 5 days after harvest kills many of the larvae and pupae of rice stem borers. In Nebraska, irrigation during dry summers provided a most favorable environment for summer to fall population increases of the European corn borer. In Texas, the use of irrigation for cotton in the more arid regions has contributed to much of the western spread of the boll weevil.

Mosquitoes and Other Aquatic Pests

Improper irrigation and drainage practices are often responsible for creating aquatic habitats for mosquitoes, biting midges, horse flies, and other insect pests of man and animals. Both engineering and agricultural phases of irrigation, including storage of water in reservoirs, water conveyance in distribution and drainage systems, and irrigation on the farm, may be involved in the development of these conditions. The solution to these insect problems must be based on source-reduction measures that will prevent, eliminate, or reduce manmade aquatic habitats. Several basic principles of source reduction of aquatic insects have been developed.

Water-distribution systems fequently create insect problems through seepage, blocking of natural drains, and impounding of waste water. These problems can be minimized by the following measures:

1. Canals and laterals should either be built in impervious soil or lined with impervious material.
2. Drains should be installed to prevent ponding of excess water, and borrow areas should be self-draining.
3. Delivery schedules should be established to provide farmers with adequate but not excessive water.
4. The distribution system should be periodically cleaned and maintained to avoid clogging, overflow, and seepage.

Serious insect-breeding problems in fields frequently develop unless proper irrigation and drainage practices are followed. These problems can be largely avoided by the following measures:

1. The farm supply system, drainage system, and field layout should be properly fitted to the topography, soil, water supply, kind of crop and irrigation requirements.
2. Surface-irrigated fields should be properly graded.
3. Only the optimum amount of water should be used.
4. Adequate drainage should be provided to remove excess water from all parts of the farm.

IMPOUNDMENTS

Manmade impoundments may range in size from small ponds of less than an acre to large reservoirs covering thousands of acres. Large impoundments are usually designed to enhance flood control, produce power, or store water for irrigation or recreational purposes. Small impoundments may be constructed to serve for detaining floods, storing logs, or stabilizing sewage, or as a source of water for livestock. Others, such as borrow pits, result from the removal of earth for construction or for filling desirably located wetlands. Most impoundments have value as habitats for fish, wildlife, and recreation, but they may also constitute favorable environments for insect pests. The magnitude of the insect problems varies greatly in proportion to the nature and extent of the favorable conditions. Emergent vegetation and floating debris, depressions subject to flooding, shallow, marshy areas, and borrow pits may be especially favorable to the production of mosquitoes (Figure 23). Horse flies, deer flies, and biting midges (Ceratopogonidae) may breed in annoying numbers along the shorelines of impoundments and marshy areas.

Insect problems associated with impoundments can be minimized by incorporating the necessary preventive measures into the design, construction, operation, and maintenance of impoundments. Problems developing in completed impoundments can be controlled by proper water management. The basic principles and procedures governing impoundment to prevent or reduce insect reproduction are as follows:

Prior to impoundage, the reservoir basin should be prepared as follows:

1. Completely remove vegetation from the normal summer fluctuation zone of the permanent pool.

FIGURE 23 Mosquitoes breed in enormous numbers in marshy, willow-choked swamps. (USDA photograph)

2. All depressions, marshes, and sloughs that will retain water at lower pool levels should be connected with the main reservoir to ensure complete drainage or fluctuation of water.
3. Deepen or fill extensive shallow-water areas.
4. Institute water-level management procedures that will minimize conditions favorable for mosquito production but will not interfere with the primary functions of the reservoir.

After impoundage, the following maintenance measures should be carried out:

1. Remove dense vegetation periodically from flat protected areas of a permanent pool by mechanical or chemical measures.
2. Construct drains in seepage areas that develop below the dam or behind dikes.
3. Periodically remove vegetation, debris, and flotage from all drains to ensure free flows.

In farm ponds, sewage stabilization ponds, and borrow pits, the most important preventive measure is the construction and maintenance of a steep clean shoreline, as free as possible of vegetation. Under such conditions, mosquito larvae have no protection, and wave action and predators will prevent their survival.

Salt marshes along the east coast of Florida, subjected to periodical flooding by tides and rain, are sources of prolific breeding of the salt-marsh mosquitoes, *Aedes taeniorhynchus* (Wiedemann), and *Aedes sollicitans* (Walker), and biting midges, principally *Culicoides furens* (Poey). Impoundment is a feasible means of minimizing both salt-marsh mosquito and biting midge breeding in certain marshes. It is necessary to keep the marsh continuously flooded by pumping, artesian wells, or streams. This limits the breeding of mosquitoes and biting midges to the water's edge inside the impoundment. Mosquito production may be completely barred by wave action and predation by minnows (Figure 24). Where only salt-marsh mosquitoes are involved, seasonal flooding of impoundments from March until September can be employed for control. Under some conditions, impounded areas may produce some *Mansonia* and other species, but their breeding can be minimized by flooding with saltwater during periods of high tides and wind tides.

FIGURE 24 Swamp cleared and impounded, permitting wave action to strand mosquito larvae and preventing the larvae from hiding from predacious fish. (USDA photograph)

DRAINAGE

Roadside ditches, borrow pits, marshes, wasteland, and lowlands in agricultural fields are sources for breeding of mosquitoes and other insect pests. These problems areas can be eliminated or reduced by the following measures:

1. Main drainage systems should be installed to remove water from irrigated and nonirrigated land (Figures 25 and 26).
2. Drainage ditches should be designed and maintained to prevent ponding in canals.
3. Ditches should be constructed to eliminate ponding outside canals that is caused by seepage or improper construction of spoil banks.
4. Drainage systems should be periodically cleaned and maintained.

ADVANTAGES AND DISADVANTAGES OF CULTURAL CONTROL

Many cultural control measures are closely associated with ordinary farm, forestry, water, and industrial pest-control management practices and there-

FIGURE 25 A 30-inch main ditch and 10-inch lateral ditch in a salt marsh. Spoil dirt is placed in piles, permitting water to flow from the marsh into the ditch. Ditch is dug to low tide level, allowing access of mosquito fish. (USDA photograph)

FIGURE 26 Improperly irrigated pasture. Ground not leveled, and water stands in one end. A drainage ditch is needed in the foreground to prevent mosquito breeding. (Photograph by Stanley F. Bailey, University of California)

fore do not usually require an extra outlay for equipment to carry out insect control. Some methods have been in use so long that farmers and other users have forgotten their derivation and the important role they play in insect control. These preventive cultural control practices are among the simplest and cheapest methods available, because they can often be carried out in connection with the usual agronomic, forest, storage, and water-management operations. Careful timing of the application of these methods to destroy the insect pest at the weak point in its life cycle is most essential. Thus, cultural control methods are advantageous because they are effective and cheap. In addition, they do not possess the disadvantages attending the use of insecticides namely, insect resistance to pesticides, undesirable residues in food and feed, and possible contamination of the environment.

The primary reason for the lack of use of cultural control measures is the need for application of preventive measures long in advance of actual insect damage. Users, therefore, may not accept them or, if they accept them, may not time them properly. Also, there may be a reluctance to use them because they do not always provide complete economic control of insect pests. Like some other insect-control methods, cultural methods may be effective against one insect but may be ineffective against a closely related species. Some methods may have an adverse effect on fish and wildlife.

It must be realized that insects are only a single factor, although a very important one, in crop production, storage and processing of commodities, and development of water resources. Therefore, any recommended cultural control method must be properly integrated with proved agronomic, forest, storage, and water-management practices. There are many opportunities to integrate cultural control with other insect-control methods. Procedures for crop and livestock production are changing, and cultural practices that were once effective for insect control may not be effective under modern production methods. Entomologists should keep abreast of new methods and initiate research projects to determine their insect-control value. They should also recognize new developments in water management and storage of commodities and adapt or develop new cultural practices to control insects. If entomological research on cultural control is to keep pace with all areas of applicability, entomologists must work cooperatively with many scientific disciplines.

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CHAPTER 11

Physical and Mechanical Control

Physical and mechanical methods are the oldest and in some cases the most primitive of all insect-control practices. They are direct or indirect measures taken to destroy the insect outright, disrupt normal physiological activity by means other than chemical insecticides, or modify the environment to a degree that makes it unacceptable or unbearable to the insect. Physical and mechanical controls are different from cultural controls in that the equipment or the action is directed specifically against the insect rather than being a normal or slightly modified agricultural or conservation practice. Physical and mechanical control methods may be either preventive or corrective.

Although some controls in this category may seem outdated, they are still sensibly practiced in various regions of the world. Some are especially applicable in the riddance of home-garden insects. However, some have been mostly discontinued because they are only partially effective; others are frequently inconvenient and expensive. The suggestion of antiquity may be misleading. Many physical and mechanical methods of insect-pest control are valid today, and research is discovering newer approaches and refined performances of the basic principles of application. Among the newer approaches, the possibilities inherent in the spectrum of radiant energy are especially promising.

Physical and mechanical controls are based on a thorough knowledge of the ecology of the insect pest and a realization that in the biology of all species there are thresholds of tolerance, such as extremes of temperature, humidity, sound, physical durability, and response to various regions of the electromagnetic spectrum. If pest ecology is conceived as the principal rational basis for all approaches to insect control, people desiring to utilize physical and mechanical methods need relevant ecological information for efficient application to the particular approach. However, too few pests are well understood ecologically. To approach these controls intelligently, it is necessary to capitalize on the possibility of modifying environments or disrupting normal physiological and behavior patterns, and to recognize the potential for incorporation of many of these physical and mechanical control methods in a planned system of pest management and control.

TEMPERATURE

Any attempt to control a population of insects by temperature manipulation must be based on a knowledge of the gross survival limits of the population. As approaches to control become more sophisticated, however, information concerning subtle physiological responses to temperature change assumes greater significance. It indicates why practices are successful, provides predictive insights, and, perhaps most importantly, shows unsuspected weaknesses and strengths in the developmental and reproductive capacity of a pest.

Insects, being poikilotherms, are mostly dependent on environmental temperatures for maintenance of activity, the effects of temperature being directed toward metabolic rates through changes in enzymatic reactivity and membrane permeability. Although certain of the social insects attempt to sustain some optimal community temperature and some flying insects perform metabolic work to bring flight-muscle temperatures up to a point where they can function efficiently, these are exceptions. Insect temperatures will not usually be more than 2 to 3 degrees different from the temperatures of their surroundings, although many insects are adapted to remain alive at apparently intolerable extremes of both heat and cold.

It is sometimes erroneously assumed that generalized protein denaturation is the key to high-temperature death, but it is unlikely that this ever becomes a problem. It is more probable that at this limit the activities of metabolic components become so deranged because of variations in reaction rates and permeabilities that they can no longer be handled by endogenous control mechanisms, and integrating activity breaks down. When this occurs, toxic metabolites build up, energy requirements are not satisfied, and irreversible degenerative processes take place. The same relationships can be invoked to describe low-temperature mortality. The conclusion derived from available data is that simplistic explanations for temperature-induced death or thresholds of one kind or another (e.g., developmental threshold, hatching threshold) have little validity. A complex of elements must be integrated for an event to occur, and a description of any single constituent as being the pacemaker is a rather naive view of the situation. A good example of this is the eclosion (pupa-adult) threshold of the black blow fly, *Phormia regina* (Meigen). Below 5°C, the perfectly formed adult will not leave the puparium, apparently because of weakened muscular contraction, resulting in a lack of fluid-filling of the ptilinum and no consequent breakout. However, the musculature is perfectly capable of total contraction at 5°C, so we must look to the nervous system for an answer, and from this to energy-liberating reactions. Simplistically, the musculature is at fault; actually, the problem is much more complex.

Generalizations at the level of mechanism do not lend themselves easily to effective specific control measures involving temperature. However, facts concerned with such things as variations in development time with temperature change and mortality temperature curves are obviously important in decision-making and control practices. There are many pitfalls, and acclimation in various species is such that submitting an infested environment to a given temperature may on one occasion cause complete riddance of the pest, while at another time it may merely decrease the infestation. The effect depends on the species and its previous environmental experience.

As a result of innumerable studies on the subject, some idea of the effect of temperature changes on a generalized population has been obtained. In a curve constructed to show relationships, the slope is small and positive throughout the temperatures at which development and reproduction rates are low and mortality is high. An accurate determination of the shape of this curve and its position on the temperature scale for a given species of pest is greatly significant in the determination of a pest exploitation of an environment.

As shown below, most of the methods presently used for controlling insects with temperature are economically wasteful, in that attempts are made to go beyond the metabolic survival limits of the pests, with concomitant damage to the components of an environment and stress on the equipment involved. It seems reasonable that physiological and ecological studies will, if properly used, aid in pest-population control by lesser but more rational alterations of the environment, leading to substantial savings to all.

HEAT

Prolonged High Temperatures

Many attempts have been made to utilize abnormally high temperatures for the control of insect pests. Insects vary in their susceptibility to heat, but no insect can survive for long when exposed to temperatures of 60 to 66°C. Lethal heat can be realistically employed by utilizing a 3- to 4-hour exposure at 52 to 55°C temperatures. In tropical regions, sunlight will sometimes accomplish control, such as when grain is dried in the sun in India, but artificial heat must normally be used in an enclosure. Damage by insects infesting stored-grain foods can be minimized by the application of heat, sometimes by special elevator heating pipes. Efficient, portable grain-drying equipment has recently been used to provide sufficient heat increase in the environment. Other examples include heat control of insects in furniture, clothing, and baled fibers; insects in logs being seasoned for lumber; insects and nematodes in soil in greenhouses; and insects in special commodities under special conditions, such as those infesting bulbs, grapes, oranges, and houseplants.

There are some very definite limitations to the heat method for insect control. Penetration of commodities requires either very long exposures or unusually high temperatures applied externally. Many plant materials cannot tolerate high temperatures. The problems sometimes associated with using heat are illustrated by an attempt to superheat military quarters for bed bug, *Cimex lectularius* Linnaeus, control. Furnaces were superheated for 8 hours, and the building temperatures were raised to 60°C. This caused the mortality of thousands of bed bugs, but great numbers of the pest survived and moved successfully to the outside walls, causing destruction of much personal property and many heating units. Bed bugs can be successfully killed by heat, however, when mattresses and bed frames are exposed to pressure-generated steam.

Radio-frequency Energy

High-frequency electric fields offer a possible physical means for control of certain types of insects, including most stored-grain species. Effects have generally been accounted for on the basis of energy absorption to a point where the internal temperatures of the insects reach lethal levels. However, some nonthermal effects may contribute to morbidity. Because of energy and equipment costs, application of this type of electric energy for insect control has not yet progressed beyond the experimental stage.

The power dissipation in a material exposed to radio-frequency (rf) electric fields is proportional to the frequency of the alternating field, to the square of the field intensity, and to the dielectric loss factor, a characteristic of the material. High field intensities (several kilovolts per inch) are usually more efficient for controlling stored-grain insects than are lower intensities (1 or 2 kV/in.). At microwave frequencies, where wavelengths are measured in centimeters and millimeters, much lower field intensities may be employed for comparable heating effects, because of the higher frequency. The frequency does not appear critical as long as it is high enough to produce the desired heating rate (above about 10 MHz), although subtle frequency effects have been noted.

Generation of rf energy requires electronic power oscillators similar to those used for radio transmitters, although usually less critical in operating requirements. Such equipment is commercially available for industrial high-frequency dielectric and induction heating applications.

Radio-frequency energy can be applied to infested grain by placing or passing the grain between electrodes to which a power oscillator is suitably connected. Both the grain kernels and the insects inside them absorb energy from the rapidly alternating electric field. The temperatures of the grain and the insects rise rapidly when appropriate frequencies and field intensities are employed. The relative heating rates of insects and grain kernels in the rf field depend on their dielectric properties. The insects will usually absorb energy at a faster rate than the grain kernels, and they can be killed without damaging the grain. For example, adult rice weevils, *Sitophilus oryzae* (Linnaeus), and granary weevils, *Sitophilus granarius* (Linnaeus), in wheat can be killed by a few seconds of exposure that only raises the grain temperature from 23 or 27°C to about 41°C. Temperatures of this order are not normally lethal to the insects, but temperatures induced by the rf electric field in the insects are believed to reach much higher levels.

Species vary somewhat in their susceptibility to control by rf electrical treatment. In general, adults may be ranked in order of decreasing susceptibility to this type of control as follows: rice and granary weevils; saw-toothed grain beetle, *Oryzaephilus surinamensis* (Linnaeus); confused flour beetle, *Tribolium confusum* Jacquelin duVal, and red flour beetle, *T. castaneum* (Herbst); the dermestids, *Trogoderma parabile* Beal and *T. glabrum* (Herbst); cadelle, *Tenebroides mauritanicus* (Linnaeus); and lesser grain borer, *Rhyzopertha dominica* (Fabricius). Species also vary in the amount of delayed mortality occurring during the first few weeks following exposures that are not immediately lethal. Most work has been done in the 1 to 100 MHz (megacycles per second) range, principally 40 MHz. Some favorable results have been obtained against cockroaches at 2,450 MHz.

Longer or more intense exposures are generally required to kill immature forms than are required for adult insects. For example, treatments producing grain temperatures of about 60°C in small samples are necessary for 100% mortality of egg and larval stages of the rice and granary weevils. When the moisture content of wheat is less than 14%, rf exposures of this order do not damage the germination or milling and baking qualities.

Although the use of rf energy is still in the experimental stage, continuing research may lead to efficient and practical methods of applying this physical method for control of certain pests.

Flaming

Flaming for insect control began in the western United States during the early 1920's, when kerosene was used as a fuel; target insects included the chinch bug, *Blissus leucopterus* (Say), and the greenbug, *Schizaphis graminum* (Rondani). It was not until the winter of 1962–1963 that interest in the method was stimulated in the eastern United States, in connection with the possibility of flaming to control the alfalfa weevil, *Hypera postica* (Gyllenhal). An accidental fire in alfalfa plots under experimentation in Georgia resulted in good weevil control. This event stimulated more intensive investigations of heat for control of the weevil, and burning alfalfa stubble in Tennessee gave encouraging control of the insect and reduced chickweed, *Stellaria media*; in these efforts, straw was used as a fuel.

Flamers have been constructed and flame cultivators have been modified for burning alfalfa during the winter. The flame causes mortality of the eggs deposited in the alfalfa stubble and of adults present in the field at the time of flaming. The resulting weevil control has enabled growers in some areas to approach first cutting before initiating chemical control or to cut early and spray the stubble.

The flaming method offers much promise for alfalfa weevil control and possibly for the control of other insects that overwinter in a crop that has a winter dormant period and thus could be burned without damage to the new crop in the spring. Propane gas has been employed as fuel for most alfalfa flamers. However, considerable attention is being given to diesel oil and other combustible liquids that show promise as fuels.

One great disadvantage of this type of heat application is the slow movement necessary during the flaming process. Best results have been obtained at a forward speed of 2 mph. Interdisciplinary research by agricultural engineers and entomologists is in progress to increase the speed and efficiency of flaming as a method of insect control.

Flaming alters the complete ecosystem of the area flamed; thus, both parasites and predators are destroyed if they overwinter in the field. However, the environment is already artificial in that it is manmade through cultivation, and possibly the native populations of beneficial insects overwinter in other sites.

Flame guns are being used in a large-scale test in the northwestern United States during the winter months, to destroy green vegetation in drainage ditches that harbor the wingless green peach aphid, *Myzus persicae* (Sulzer). The destruction of the overwintering host plants and aphids prevents the development of winged aphids that would later fly to sugarbeet fields, where they could transmit the yellows virus of sugarbeets. Additional research is needed to determine more precisely the conditions under which flaming may be used as a practical insect control measure.

COLD

One of the most important factors governing abundance and distribution of insects is cold. In the case of insects incapable of hibernation, low temperature is usually the most important factor in restricting the extension of range and preventing the establishment of populations in areas into which they are accidentally introduced by man.

Low temperatures may be effective in reducing the economic loss caused by some insects. Many insects are subject to severe winter mortality. In some instances, as high as 90 to 100% of the population of a given species has been destroyed by severe winter temperatures. Even cool weather in the summer may have a profound effect in reducing the damage of certain insects by slowing their rate of development and consequently reducing the number of generations per year.

There are certain types of situations where it is practical to use low temperature in the control of insects. To modify the environment to this end, it is imperative that the insect population be restricted in such a manner that control may be effected either by manipulating the temperature, or by exposing the total population to the desired temperature, or both. In certain instances it may be more practical to lower the temperature to a level at which development of the insects is retarded and little damage is done than to attempt to lower it enough to kill the insects.

Some useful applications of cold have been in the protection of stored grain and other stored products from insect pests. Since most of the pests of these products are of tropical origin, they are usually extremely susceptible to low temperatures.

In northern climates and at high elevations where seasonal subzero weather occurs, excellent control of insect pests has been obtained by opening flour mills and allowing them to cool down to outside temperatures. The degree to which the cold penetrates the product is principally dependent on the length of exposure time. When the outside temperatures are -22°C or lower, 24 to 36 hours of exposure are usually recommended. (All steam lines and all receptacles containing liquids that might freeze must be drained.)

Stored seed may be protected by exposure to temperatures between 4 and 10°C, since most grain-infesting insects are inactive at these temperatures. It is important that conditions of low moisture be maintained in this situation, because grain-infesting mites may damage seeds at these temperatures if the moisture content is over 12%.

The storing of apples at 0°C under normal conditions and at 0 to 3°C in controlled atmosphere (3% oxygen and 2 to 5% carbon dioxide) provides, in addition to high quality of the fruit, excellent insect control. A 60-day exposure under either of these conditions is lethal to all larvae of the apple maggot, *Rhagoletis pomonella* (Walsh), and a 33-day exposure is lethal to larvae of the plum curculio, *Conotrachelus nenuphar* (Herbst). In both cases it is the cold that is lethal. After 90 days of cold storage, apples grown in the northeastern United States can pass quarantine for shipment into California.

Low temperature is being used to prevent the reintroduction of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), and the introduction of other fruit flies into the United States. Fruit imported from countries infested with these fruit flies must be refrigerated at 1 to 2°C for 12 to 20 days, the exact period depending on the species of fly involved. Precooling to the desired temperature must be accomplished before the shipment leaves the country of origin. This treatment will kill fruit fly eggs, larvae, and pupae.

Cold can be used to kill drywood termites in furniture. Exposure in vaults for 4 days at -9°C is effective. In northern climates, drywood termites that gain entrance from accidental introduction do not survive the natural cold except in localized, artificially heated structures.

Refrigeration is employed commercially for summer cold storage of furs and fabrics susceptible to insect attack.

HUMIDITY

Insects must maintain a level of internal water within reasonably narrow limits; this level is strongly influenced by external factors. Although homeostasis is well known in termites (one of the chief functions of the nest is to maintain a constant high humidity), most forms of insects cannot modify their microclimate and must react to adversity by moving to a more favorable environment.

The moisture relationships of terrestrial insects can be understood most easily by studying the atmospheric humidity where these organisms live. Insects as a group are often cited as animals that have been especially successful in establishing themselves as terrestrial organisms, and in arid regions they are an elite assemblage of animals. Despite their small size, which produces problems of water conservation because of a high surface-to-volume ratio, insects are quite resistant to desiccation because they possess a highly impermeable cuticle, lose little water in the excreta, and have some ability to utilize metabolic water. They occupy an unbelievably wide range of humidity conditions, from extremely dry to near saturation. No single species spans a wide spectrum of such a gradient, although each has its own definable preferendum, which may vary for each life stage. Generally, insects inhabiting an extreme of a moisture gradient cannot survive under the opposite condition but may do so in a particular life stage; e.g., puparia of the Hessian fly, *Mayetiola destructor* (Say), may survive up to 5 years in a dry environment until conditions are conducive to adult survival.

The general gross effects of humidity on insects can be thought of in terms of distribution, activity, longevity, fecundity, mortality, and speed of development. Humidity can also influence phenotypic expression. For example, color is determined by moisture relationships according to Gloger's rule, which states, in general, that populations of an insect species in cool dry regions are lighter in color than those in warm humid areas, but pigmentation increases in cool humid climates and decreases under hot dry conditions. Experimental work has elaborated humidity responses of many insects. When correlated with field observations, such studies aid in the understanding of behavior patterns and distribution, in both time and space.

Results of several studies epitomize the sort of information that exists for some pest species. One such work is concerned with the wireworms, *Agriotes obscurus* (Linnaeus) and *A. lineatus* (Linnaeus), where humidity assumes a crucial role in behavior. Wireworms represent a group of insects favored by high moisture levels; in fact, the species studied avoid dry air. The experimental preference is 100% relative humidity, as demonstrated by the fact that other humidities are avoided when saturated air is available. Conditions in the soil provide humidities near saturation, and, at such a range, the responses of the insect are most sensitive; because of the need for high moisture, greatest sensitivity to the higher levels is an especially useful survival mechanism. Experimental evidence of humidity reactions can be correlated with real conditions of wireworm behavior in the soil; observations of migration of wireworms away from the surface strata during periods of drought suggest that low humidity is an important and limiting factor of the environment. Reduction of moisture level in the soil can often be realized through cultivation.

Two sawflies, *Neodiprion americanus banksianae* (Rohmer) and *N. lecontei* (Fitch), react to gradients of evaporation rate by aggregating at the highest rates (low humidities). This explains the presence of larval colonies of these coniferous pests on the most exposed portions of trees situated in the more open parts of a stand. Effects such as this have implications for surveys and sampling as well as for control.

Humidity sometimes has profound effects on whole populations. For example, in marginal habitats, when humidity approaches the minimum tolerance, a notable decrease in the abundance and distribution of certain species can occur. Such a phenomenon is exemplified by the pale clouded yellow butterfly, *Colias hyale* Linnaeus, which commonly migrates, in the summer season, from the European continent to Great Britain. The insect would be expected to overwinter in England because of temperature tolerances, but it has not done so. It is quite certain that humidity is the major factor preventing this species from permanent colonization.

Analyses of populations of the 2-year cycle spruce budworm, *Choristoneura fumiferana* (Clemens), have been made with regard to evaporation. Largely because of structure, stands of spruce in which outbreaks had occurred were characterized by evaporation rates consistently higher than those in nonoutbreak stands with a similar composition of host species. In this case, humidity is an essential factor in population limitation from two viewpoints: nonoutbreak areas with increased humidities favor greater mortality because of the fungus disease organism *Beauveria bassiana* (Bals.) Vuill.; and high humidities cause behavioral anomalies resulting in inactivity such that normal feeding, spinning, and molting cannot occur.

Humidity can be plotted in conjunction with other factors (usually temperature) to produce multidimensional models of development. When contours are drawn, a configuration of equal zones of response becomes available. Such systems have great predictive value and have been successfully used for pests such as the boll weevil, *Anthonomus grandis* Boheman; the African locusts, *Locusta migratoria migratorioides* Reiche and Fairmaire and *Schistocerca gregaria* (Forskal); the rice weevil; and the lesser grain borer.

The spruce budworm (1-year cycle) is well adapted to the moisture gradients in its environment. Each stage of the insect reacts to moisture differences, so that the site it uses is also the place where survival probability is the greatest. Although the behavior of the budworm is a complex pattern involving responses to several factors, the humidity component can be partitioned to yield an understanding of behavior in the field. With this insect, zones of preferred temperature do not exist in the host area; rather, larvae always respond to the rate of evaporation. Following hatching, larvae seek a site to form the overwintering hibernacula. Survival depends on their having a hibernaculum place that is neither too wet nor too dry. Newly emerged larvae cannot spin in atmospheres outside the preferred humidity range. When second-instar larvae emerge from the hibernacula, they may find and penetrate needles or buds. A bimodal humidity response governs their behavior at this stage; high evaporation rates are associated with greatest crawling rates, and the larvae actively move away from places of high evaporation. A secondary crawling-activity peak consistently occurs in air that is nearly saturated. Such responses allow a better chance for distinguishing opening buds, which produce a layer of higher vapor pressure than the air surrounding old foliage. Final-instar larvae live in feeding tunnels characterized by humidities very similar to the preferendum. When feeding begins to exhaust the nutrient supply, the feeding tunnel opens and external air penetrates, the changes resulting in increased evaporation rate. The larvae are stimulated to crawl away from this changing environment just as larvae on defoliated twigs are stimulated, because of high evaporation rates, to drop on threads until foliage is encountered on the way down.

Physical factors such as humidity should be included in considerations of dynamic climatology related to entomology. Extensions of the above studies characterize such research for several forest pests. When a dominance of continental polar and maritime polar air masses, which yield dry sunny weather, is present for several years, a favorable situation is provided (other factors being nonlimiting) for the development of spruce budworm populations. In the same geographical areas where the budworm is a pest, another defoliator, the forest tent caterpillar, *Malacosoma disstria* Hübner, attacks hardwood stands. When the spruce budworm is abundant, the tent caterpillar populations are favored when a predominance of warm, humid, partly cloudy weather from maritime tropical air masses recurs for several years. Thus, these two pest species have alternating high densities in a given region.

It is possible to manipulate the habitat so that conditions are unfavorable for the development of damaging populations of some insects. A brief account follows of several cases where such modifications are commonly employed.

Early in the twentieth century, the relationship of white-pine weevil, *Pissodes strobi* (Peck), populations to stand structure was empirically acknowledged when it was observed that hosts growing in open situations were more susceptible to weevil infestation than were shaded trees or trees cultured under a dense plantation format; only recently has the pest ecology been well elucidated. Although not independent of temperature interactions, white-pine weevil activity—feeding of adults, oviposition, and copulation—is restricted to rather narrow limits of relative humidity. At one time white pine was selected against in planting programs because of the serious impact of the weevil on salabity of timber, but it is now a common practice to plant weevil-susceptible hosts in a hardwood stand. The existing canopy provides a modified environment unfavorable to weevil activity, because humidities generally exceed the low levels required and temperature regimes are lower than necessary for population development.

Humidity of the habitat is also important with pests such as subterranean termites; corrective measures frequently include drying of the air beneath infested structures by improved ventilation. Although subterranean termites usually depend on soil contact, they frequently find favorable sites for establishment in synthetic environments provided with excess moisture by leaks and condensation. Correction of such problems to reduce humidity in the microenvironment is required to eliminate the infestations in buildings.

Insect damage caused by stored-grain pests increases to a given point with the moisture content of the grain. Such a phenomenon provides part of the rationale for holding the moisture content of grain low (below 12%).

Tropical species of *Drosophila* are greatly influenced by atmospheric humidity. *D. melanogaster* Meigen, a common fruit fly of importance in commercial tomato production, has been carefully studied in this regard. Humidity imposes the main influence on adult activity, and high levels favor oviposition. The potential of damaging populations of *Drosophila* can be reduced by maintaining tomato fields free of weeds and by selecting varieties with an open type of growth. In a microclimate resulting from dense foliage, these flies are active throughout the day, with oviposition common at dawn and dusk.

VISIBLE AND NEAR-VISIBLE RADIANT ENERGY

LIGHT TRAPS

Devices employing the use of radiant energy are utilized in six principal ways in insect control: at ports of entry to detect the presence of imported noxious insects (detection traps); to determine the spread and range of recently introduced pests in a region (survey traps); to determine the seasonal appearance and abundance of insects in a locality, and the need for the application of control measures (survey traps); to evaluate the effectiveness of control measures (survey traps); to control insects *per se*; and to supplement other control measures.

Light Emission

The use of light traps for insect control is based on the photopositive response of many insects. Although numerous sources of radiant energy, such as kerosene, gasoline, and acetylene lamps, have been utilized in the study of the phototactic responses of insects, the electric lamp is the principal source used in insect-control studies.

The term "light" is a partial misnomer in that electric lamps may emit wavelengths in the invisible ultraviolet and infrared as well as in the visible regions of the electromagnetic spectrum. The known limits of the radiant-energy spectrum extend from wavelengths of 0.0001 Å to 100,000 miles and from frequencies of 1.6 to 10^{24} Hz. Electric lamps produce wavelengths from 1,800 to 50,000 Å (Figure 27), a very small portion of the electromagnetic energy spectrum. The portion of the spectrum produced by electric lamps is divided into three regions with no sharp lines of demarcation; there is a gradual change from one region to another. These regions are the ultraviolet (1,800 to 3,800 Å), the visible (3,800 to 7,600 Å), and the short-wave or near-infrared (7,600 to 50,000 Å). The ultraviolet region is divided into the far (1,800 to 2,800 Å), the middle (2,800 to 3,200 Å), and the near (3,200 to 3,800 Å) ultraviolet. The visible part of the spectrum is divided into violet (3,800 to 4,300 Å), blue (4,300 to 4,900 Å), green (4,900 to 5,600 Å), yellow (5,600 to 5,900 Å), orange (5,900 to 6,300 Å), and red (6,300 to 7,600 Å). The portion of the infrared region of the radiant spectrum beyond that produced by electric lamps is known as far infrared.

Electric lamps include incandescent lamps (tungsten filament lamps) and various gaseous-discharge lamps employing mercury vapor and other gases, such as argon, neon, and xenon. The incandescent lamp has a continuous spectrum. The energy radiated in the visible spectrum is lowest in the violet

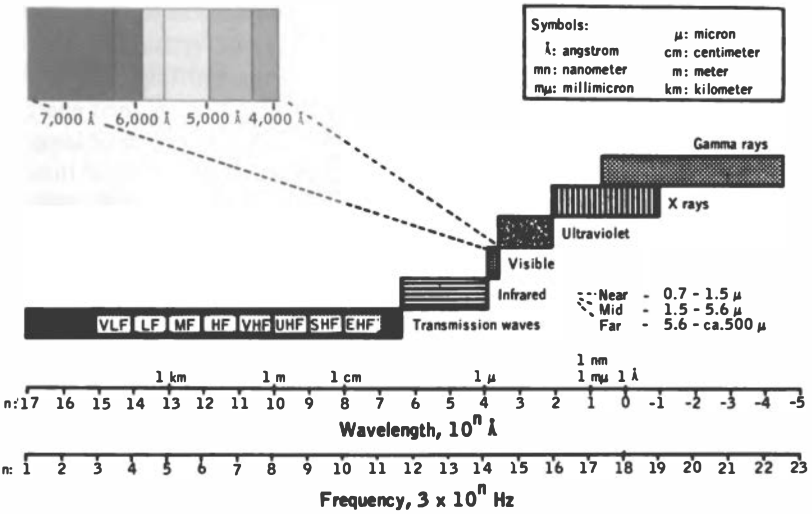

FIGURE 27

blue and highest in the red. The major portion (75 to 85%) of the energy input to the lamp is radiated in the near-infrared region. The mercury-vapor lamp produces a line spectrum, seven in the ultraviolet and four in the visible spectrum. The argon glow lamp, which consists of a mixture of gases, produces a divided spectrum (2,800 to 5,000 Å and 6,000 to 7,600 Å) but radiates mainly blue and violet and in the near-ultraviolet region. Neon lamps radiate mainly yellow, orange, and red. The fluorescent lamp employs a phosphor to convert part of the radiation produced by the mercury-vapor arc to a bank spectrum peaking at some longer wavelength. The wavelengths produced are limited to the reradiation characteristics of particular phosphor materials. The envelope of the blacklight (BL) fluorescent lamp, which is very attractive to most photopositive insects, is coated with a phosphor that inverts the 2,537 Å line of the mercury arc to 3,650 Å. The blacklight blue (BLB) fluorescent lamp differs from the BL in that it has an internal red-purple filter that absorbs most of the visible light radiated by the BL lamp. BL fluorescent lamps are the most commonly used in light traps; they are readily available as linear (more attractive and reliable) and circular lamps.

Lamp Attraction

The attractiveness of electric lamps to photopositive insects depends on the wavelength and the amount of energy (radiant power) emitted, the intensity (brightness), and the size of the source.

Although photopositive insects are attracted to wavelengths in all portions of the ultraviolet and visible spectrum, and presumably to certain wavelengths of the infrared, most species are more attracted to lamps emitting wavelengths in the middle- and near-ultraviolet regions than to those emitting their energy in other regions. The order of attractiveness (from greatest to least) of lamps to most species of photopositive insects is to those which emit most of their energy in the near ultraviolet (BL and BLB fluorescent lamps), middle ultraviolet (sun lamps), blue, far ultraviolet (germicidal lamps), green, yellow, and red. Many species of beetles and some species of leafhoppers and moths are more attracted to green. A few species of flies are more attracted to red and a few to far ultraviolet. Some species of insects, e.g., the honey bee, *Apis mellifera* Linnaeus, the pink bollworm, *Pectinophora gossypiella* (Saunders), and the potato leafhopper, *Empoasca fabae* (Harris), are attracted to two different regions of the spectrum. For instance, the peak response of the pink bollworm moth at a low level of intensity is to green, with a secondary peak of response to near-ultraviolet wavelengths. When the energy level is doubled or quadrupled, however, the peak of response shifts from the green to the near-ultraviolet region.

The term "intensity" as used in the study of insect responses to electric lamps involves two characteristics: brightness (luminous intensity) of the source, and the luminous flux density (illumination) that an object (the insect) in space receives. Since lamps of high brightness also produce high levels of luminous flux density, the influences of these two characteristics on the attractiveness of a lamp are difficult to separate. However, the attractiveness of a lamp to insects increases with increases in the brightness and illumination above the threshold of response to a point of optimum attractiveness and attractiveness and then decreases. This change in attractiveness is not proportional to the energy output or input. Experiments have shown that the activity of nocturnal insects ceases in the vicinity of a very intense source (10,000-W lamp) and that diurnal insects become active. Moths approaching such a source drop to the ground at some distance from the lamp and remain unresponsive and immobile until darkness returns; the reaction resembles that of catalepsy.

The brightness of a lamp is affected only by changing the amount of luminous flux emitted. Incandescent and mercury-vapor lamps increase in brightness with increase of wattage input. Fluorescent lamps, which increase in physical size in almost direct proportion to their wattage input, are of relatively the same brightness in all sizes. Luminous flux density is affected by anything that increases the total radiant-energy flux through space. Different illumination levels can be achieved by using multiples of similar lamps without altering the source brightness. However, changing the brightness of the lamp may not alter the illumination. Such a change is dependent on the size of the source.

An increase in the physical size of the light source increases the number of insects attracted up to an optimum, but not in proportion to the increase of the physical size.

Light-Trap Design and Placement

Light-trap designs vary with the purpose for which they are to be used. However, all light traps consist of two essential parts: a lamp and a collecting or killing device.

General-Survey and Detection Traps General-survey and detection traps are commonly equipped with a 15-W linear BL fluorescent lamp mounted over a funnel leading into the collecting or killing chamber. Since the insects collected must be in good condition for identification, it is essential that water be excluded from the collection chamber and that the insects be killed quickly, so that they will not become mutilated.

Traps of two kinds (Figure 28) used for survey purposes are classified as omnidirectional, in which the lamp is exposed to view from all directions, and unidirectional, in which the lamp is exposed to view from one direction only.

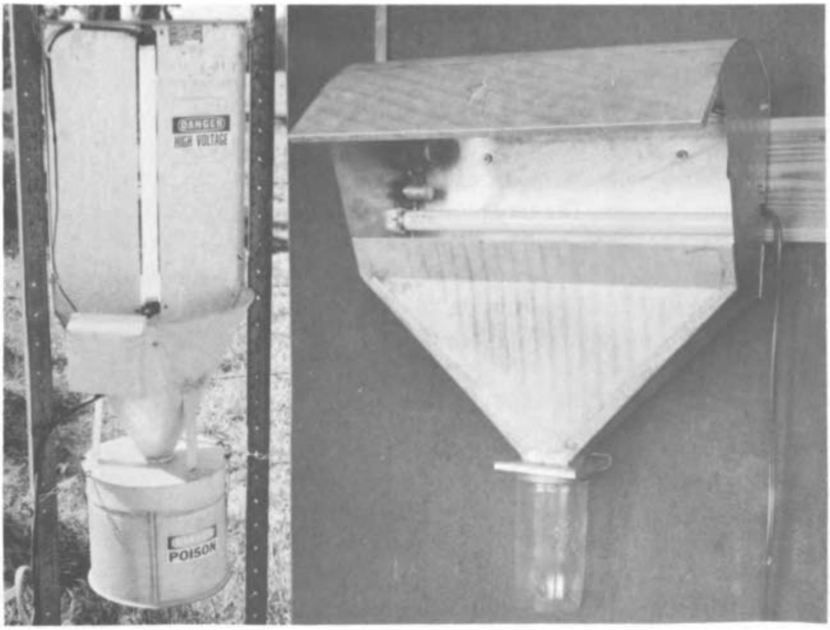

FIGURE 28 **Blacklight fluorescent traps used for insect survey and detection.** ***Left*****: omnidirectional.** ***Right:*** **unidirectional.**

Omnidirectional traps collect two to four times more insects than unidirectional traps, but the number of species collected is about the same in both types. The killing chamber may be a glass jar or a can fastened to the bottom of a funnel; drainage must be provided. General-survey and detection traps are not equipped with a fan to draw the insects into the funnel and force them into the collecting chamber, because of the danger of mutilating the insects and making their identification difficult or impossible.

The common killing agents used in the collection chambers are calcium cyanide and ethyl acetate. The calcium cyanide is usually put into a porous container, such as a paper bag, which is placed in the bottom of the chamber. It should be renewed each day. The amount used depends on the size of the chamber. When ethyl acetate is used, the collection chamber is frequently lined with a coating of plaster of Paris, which absorbs the liquid.

Specialized survey traps have been designed for a number of different insects. Among the more common ones are the New Jersey mosquito trap, the cigarette beetle trap, the pink bollworm trap, and the European chafer trap. The New Jersey mosquito trap is equipped with a fan and a 25-W incandescent lamp. The pink bollworm trap is equipped with three 2-W argon glow lamps because these lamps attract a smaller number of other species.

The survey and detection traps commonly used in the United States are designed to operate from standard 115-V, 60-cycle alternating current. When no electric service is available, as in forested areas, automotive-type storage batteries used in conjunction with static inverters have proved to be the best portable power supply. A 6-W instead of a 15-W BL lamp is commonly used in these portable, battery-powered traps.

The traps are generally mounted or suspended so that the lamp is 4 or 5 feet above the ground. The trap location in relation to particular crops and other vegetation, and to buildings and other obstructions, influences the numbers and kinds of insects collected. For a general survey of agricultural pests, the traps are usually placed in an open area having low ground cover; for specific crop-insect information, they are located near the crop in question.

The use of survey light traps and their relationship to other methods of population evaluation are discussed in Chapter 3.

Control Traps Two kinds of traps are used for the control of agricultural pests. In one the design is much the same as that of the omnidirectional survey trap. The trap is equipped with a fan to draw small delicate insects into the funnel and force them into the killing chamber. The funnel is mounted so that it empties into a large container, such as an oil drum, that is partially filled with water and diesel oil, or into a large container that confines the insects until they die.

In the other common type of control trap, the lamp (or lamps) is attached to an electric grid, which may be flat or a hollow cylinder surrounding the lamp. The flat grid is the most commonly used (Figure 29). Such devices have been used in experiments on the control of agricultural pests and are commonly used in warehouses, factories, and other industrial establishments, and for reducing the number of insects in outdoor-use areas. The main disadvantage of the electric-grid type of trap when used outside is that so many insects may be attracted to the lamps that the grids are shorted-out and, as a consequence, the insects are not killed. Another disadvantage is that large moths and beetles that strike the grid may not be killed but may be merely stunned and fall to the ground, where they recover.

In experiments with light traps for the protection of corn from the European corn borer, *Ostrinia nubilalis* (Hübner), the best results were obtained by placing the traps within the field to be protected rather than at the edges of the field. In experiments on controlling tobacco hornworms, *Manduca sexta* (Johannson), over a large area, promising results have been obtained by placing the traps at preselected distances without regard to the particular crop concerned. Individual tobacco fields can be protected equally by placing the

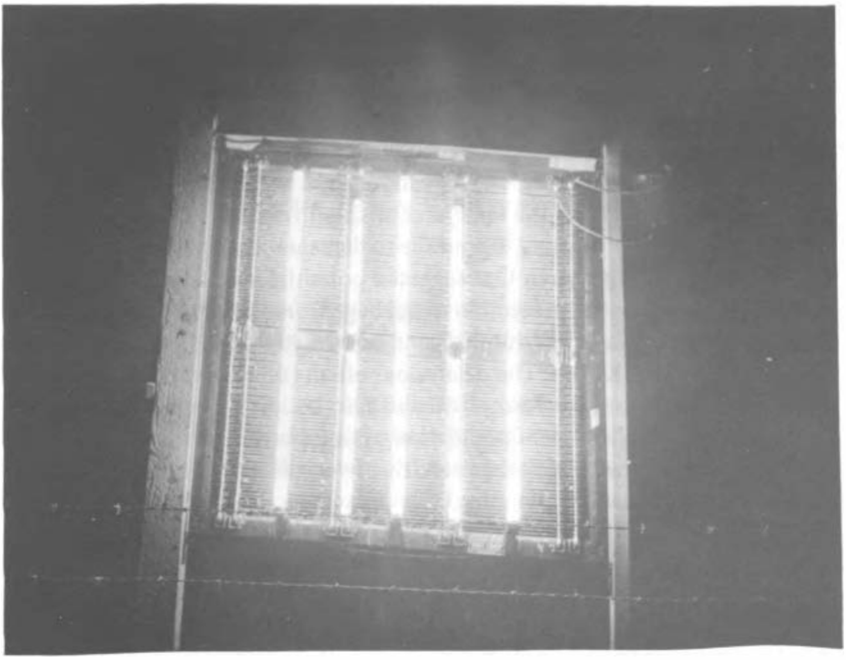

FIGURE 29 Night view of electric-grid light trap.

traps at the edge of or within the field. However, placing the traps at the edge of the field reduces the protected area by half.

Protection of Growing Crops

To use light traps to protect plants from immature or wingless adult insects, or both, either the winged females must be captured before they have oviposited on the plants or the males must be caught before they have mated. When winged adults are injurious, the traps function by capturing the insects as they fly into the field or by attracting them away from the plants. In some cases, the radiant energy emitted either repels the insects (winged aphids) or irritates them so that they are restless and feed little, e.g., striped cucumber beetles, *Acalymma vittatum* (Fabricius). Since not all species of insects are phototactic, light traps are not a panacea for every injurious insect, but evidence is accumulating that they are finding their place in a variety of situations.

The radiant energy emitted from BL lamps is highly attractive to the moths of the tobacco hornworm and the tomato hornworm, *Manduca quinquemaculata* (Haworth). Research in Indiana led directly to recommending the use in that state of one 15-W BL trap per acre for the protection of tobacco plants in 1958; this practice has been employed successfully ever since. This approach to control was extended to greater tobacco acreage in North Carolina, utilizing a 113-square-mile area. Three traps per square mile, in combination with stalk-cutting and insecticide treatment to prevent late-season breeding of hornworms, reduced infestation in the tobacco about 80% in the center of the area the second year. About 20 times more males were captured in traps in which virgin female moths had been placed than in light traps operating during the same time without females; these results suggest the possibility of using this means to decrease mating in the field.

Other examples of research that suggest a potential use of BL traps for insect control include the protection of cabbage from the attack of the cabbage looper, *Trichoplusia ni* (Hübner), and of celery from the celery looper, *Anagrapha falcifera* (Kirby). The deleterious effects of both the European corn borer and the corn earworm, *Heliothis zea* (Boddie), can be significantly reduced by light traps if population pressure is not extremely high. Damage to tomato fruit and foliage resulting from the attack of tobacco and tomato hornworms can be minimized. The increase in yield of cucumbers from plants protected by light traps has been especially encouraging; populations of the striped cucumber beetle and the spotted cucumber beetle, *Diabrotica undecimpunctata howardi* Barber, were reduced, and the transmission of bacterial wilt was minimized. Such benefits from the use of light traps eliminate the need for numerous chemical applications in those climatic areas where light attraction is consistently good (Figures 30 and 31).

FIGURE 30 Cucumber plants protected by blacklight trap are relatively free of bacterial wilt spread by cucumber beetles.

Light traps may be used as an attraction mechanism to bring moths into contact with chemosterilants and then permit release back into the environment.

Not all moths and flying beetles are sufficiently attracted to blacklight sources to effect control, and populations over extensive areas are not easily manipulated. Care must therefore be exercised in recommending these devices.

The main limitations associated with the use of light traps to protect agricultural crops are: availability of electric power, initial investment, and the presence of pests that require other controls because they are not photopositive. The advantages of the use of light traps are: they leave no residues on crops; they operate continuously, thereby eliminating the necessity of timing of control applications; they will attract irrespective of the physical condition

FIGURE 31 Cucumber plants near those shown in Figure 30, but not protected by a blacklight trap. Cucumber beetles were active and spread bacterial wilt that destroyed the plants.

of the field; their use may be integrated with other approaches to control; and the cost of operation is low.

Insect-free Lighting

Well-designed light traps are helpful in alleviating the problems caused by nocturnal insects that are attracted to lights used for illuminating outdoor areas such as patios, drive-in restaurants, swimming pools, and golf driving ranges. Placement with regard to the total area and the existing lighting requires individual study if the traps are to be effective. Insect-free lighting is often more effective than traps alone. This concept involves the use and proper placement of nonattractive lamps (yellow) for illumination in the actual area to be protected and the use of BL traps to draw the insects away from this area. The BL lamps are usually placed at a distance of approximately 50 feet from the area to be protected. This concept can be extended to pest management in and around manufacturing plants where night-flying insects frequently contaminate products.

Traps to Control Flies

The possibility of using light traps to control several species of flies in dairy barns where insecticide use is restricted is encouraging.

The house fly, *Musca domestica* Linnaeus, the most common species in this habitat, is more attracted to BL lamps than to other kinds. In barns, the flies are most attracted during the period from one-half hour before to one-half hour after sunset.

SHORT-DURATION LIGHT

Brief intense "flashes" of radio waves, infrared, visible, and ultraviolet radiation often have effects different from those of the same quantity of radiation administered slowly. Although the mode of action is not understood, it is now clear that such flashes are a promising way of producing a given effect and that in some cases an "energy barrier" for chemical effects is probably overcome. Electronic photoflashes similar to those employed by photographers have been used experimentally in this way to kill or sterilize laboratory insects or to prevent their diapause.

In nature, the possibility of regulating light duration, intensity, and spectral composition seems slight. Reactions of many species of insects to the seasonal changes in day length are well known. One of the most important reactions is the inducement of diapause, a form of developmental inactivity. This physiological condition allows the insect to survive such adverse influences as winter cold, dry spells, and excessive moisture. The insect in a dormant, nonfeeding, or otherwise resistant state can pass an adverse period of time and resume activity when suitable conditions reoccur. One of the most familiar forms of diapause is hibernation to survive cold periods.

The insect, in response to changes in light duration, angle of incidence, or intensity, may cease feeding or egg-laying, or otherwide modify its activity. If this reaction could be artificially induced, the regular cycle of an insect might be drastically disrupted and cause, for example, the production of eggs (and a new generation) at a time of the year when the insect would normally seek shelter as an adult. This would be a catastrophe to the population of insects involved and would result in severe mortality. Research attempts to produce such population disruptions have been successfully undertaken in artificial environments. However, no practical control measures involving light regulation and its subsequent effect in insect-population control are presently being practiced.

Another approach to light regulation is the possible use of strategically timed photoflashes. Some insects, during their immature development, require a photophase of a given duration to promote diapause. This is followed by a phase in which light suppresses diapause. In the imported cabbageworm, *Pieris rapae* (Linnaeus), the use of photochemical reaction appears to regulate hormone activity. When larvae are exposed to short electronic flashes scheduled 3 to 4 hours after the end of their normal photophase, a high percentage of pupae bypass diapause. If it is found that similar light-induced disruption of normal development patterns is common among insect species, such a technique could conceivably place the pest out of normal synchronization with favorable ecological conditions and result in mortality.

RESPONSE TO INFRARED

Very little is known about the response of insects to infrared radiation. Most research in this area has been concentrated on heating and killing the insect with infrared radiation. Infrared radiation is often wrongly termed "heat radiation" because it generates heat in any absorbing object in its path; however, so do all other light rays and high intensity radio waves. Because the infrared band falls between the bands of visible light and radio ($0.75\ \mu$ to $10^3\ \mu$), it is an extremely intriguing area of the spectrum and demonstrates many of the characteristics of both visible light and radio waves.

Theoretical work presently being conducted indicates that the spines of certain insects and some other sensory mechanisms may be capable of tuning in to infrared radiation. These spines would function as dielectric-type antennas in the same manner as metal antennas in the radio region. It has already been demonstrated in the laboratory that spines on the antennae of saturnid moths are capable of detecting far-red radiation, which is very close to the infrared frequencies.

Infrared radiation is also generated by the vibration and rotation of atoms and molecules. These bands are being investigated with the idea that such narrow band radiation lines can be amplified in the manner of lines given off by lasers and then amplified to control the behavior of the insects.

If the theories concerning the emission of scent molecules are correct, it should theoretically be possible to enclose chemical scent attractants in an infrared or microwave amplifying system and stimulate the scents with electrodes or other radiations. This would cause increased excitation and greater emission from the molecules and in essence the system would be an emitter that could become a permanent part of a species insect trap.

An infrared light trap that attracts mosquitoes has been developed. If the frequencies involved can be further isolated and amplified, a physical control system can be developed, and it might eventually be possible to construct more efficient species traps by utilizing special infrared and visible wavelengths. Such traps would probably consist of high-energy, short-wave emissions alternating with longer, wave-tuned frequencies for different insects.

There are other ways in which infrared radiation affects the physical being of insects, including, for example, the apparent need for low levels of infrared radiation during growth and development of some species.

LIGHT REFLECTION

Aluminum foil has demonstrated great potential as a control device for certain aphids. Small-plot field experiments by several workers have employed sheets of reflective aluminum among growing plants to repel aphids effectively from the "protected" plants. The future implications of this method and the insect response involved are under study.

LASER PHENOMENA

"Light amplification by stimulated emission of radiation" is employed successfully in microsurgery and could conceivably be used to bring about desirable genetic modification of insect host material and, in some cases, of the insects themselves. The laser is effective because it can produce a powerful pencil beam of light or infrared energy at precise wavelengths, and this makes it presently unsuitable for all but the most sophisticated techniques of insect control. There is no evidence of a "death ray" at any particular wavelength, but such a discovery would undoubtedly have a significant effect on insect control.

SOUND

The use of sounds for insect control has long been regarded as a possibility, but results of the few practical tests that have been made have been disappointing. Three basic methods have been suggested: use of very-high-intensity sounds for physical destruction; use of loud noises to repel the pests; and use of recorded sounds produced by insects, or imitations of these, to influence behavior.

The energy of very-high-amplitude sound fields (140 to 160 dB, *re* 10^{-16} W/cm^2) can kill insects, either by mechanical destruction or by conversion into heat through absorption. Harmful effects of very intense underwater sound fields, usually ultrasonic, have been particularly well investigated, although not with insects. Similar effects of intense airborne sounds are less well known. In both cases, the equipment needed to produce the sound is expensive and cumbersome, and the sound fields are very restricted in extent. Generally, if the insects are in such a small field, it is much cheaper to control them by other means. Wood-boring insects or stored-product pests might be killed by solid-borne ultrasonic sounds, but no practical tests have been reported.

High-intensity sounds (100 to 130 dB), particularly noises, might repel certain insects, but no positive results have been reported. The use of loud noises produced by fireworks and mechanical devices to repel birds has been only moderately successful, for the birds rather rapidly become tolerant of these sounds. The same thing could happen with insects, although differences between the two groups in sound reception may make such a comparison inapplicable. Further, unless these loud noises were ultrasonic, irritation to man or domestic animals could also be a factor.

Most promising for possible use in insect control are acoustic communication signals, either recorded from the insects themselves or produced artificially. These signals are active at low intensities (often just a few decibels above ambient noise levels), therefore being economical to broadcast; they are usually fairly specific in action, thus allowing selectivity. Although sound recording and projecting equipment is expensive, the cost might be spread over some time, because, if properly engineered, it could be effective for a number of years. Recorded communication signals, therefore, could very well be economically practical.

Three uses for communication signals seem promising: to attract insects to a trap, to repel them from specific areas, and to jam their natural communication systems.

There have been many studies on sexual attraction by sounds in Orthoptera (Gryllidae, Tettigoniidae, and Acrididae) and Diptera (Culicidae), and a large reservoir of fundamental information is available. With orthopteran sounds, unfortunately, no one has provided even pilot-scale field trials, despite some attempts. With mosquitoes, attraction of males in the field by play-back of recorded sounds of females has been reported, but large-scale tests have not been made. In this case, only males were attracted, and they do not bite. In every case of attraction, the broadcast sounds must compete with the natural sounds, and they cannot be too loud or they repel near the sound source. Thus, many loudspeakers are needed if a large area is to be covered, and this is costly. Certainly, repellent sounds, if they could be found, would be more desirable, but so far there are no reports of field tests, or even promising laboratory tests, utilizing this approach.

Jamming a natural communication system has been tried with certain noctuid moths. These moths have tympana that are especially sensitive to ultrasonic sounds such as are used by bats to navigate and to locate prey; this sensitivity enables some moths to escape capture by pursuing bats. Sounds like bat sounds cause the flying moths to drop from the air. Broadcasts of recordings of these sounds have been tested as an acoustic fence around areas, and the tests seem promising. If such broadcasts prove useful, several problems of acoustics will probably arise, such as sound shadows and attenuation, and their solution will require considerable study.

In the case of chemical sexual signals, it has been suggested that communication systems of insects could be jammed by mass dispersal of the chemicals. The same difficulties seem possible as with attraction; the sounds must be at nearly normal intensities, and large areas must be covered. Unless dramatic reductions in population were obtained, the expense would probably be prohibitive.

For the following insect groups enough is already known about acoustical reactions to give reason for belief that controls by means of sound might be developed:

1. Grasshoppers and crickets. Many studies have been made on all aspects of acoustical behavior and on the nature of the sound signals; these insects use sounds for sexual and territorial signaling, at least.
2. Cockroaches. These insects respond to vibrations, and some produce sounds; otherwise, their acoustical behavior needs much more study.
3. Hemiptera, e.g., *Triatoma* spp. Highly identifiable sounds are produced; duplication of these sounds might be used to lure the insects to their death.
4. Flies and mosquitoes. Mosquitoes are discussed above; wing sounds, at least, seem to be communicative; many of these insects respond to sounds.
5. Moths and butterflies. Moths have been discussed; some moths have tympana and some produce sounds; communication by sounds, however, is not certain; larvae and adults generally respond to sounds of sufficient intensities.
6. Termites and ants. Some species stridulate, and all seem to be sensitive to vibrations; communicative significance of the sounds they produce is uncertain.
7. Beetles. Many species stridulate; most are sensitive to vibrations, at least; communication by stridulatory sounds has been observed, and future research may lead to new approaches to control.

The general prospects for use of sounds in insect control is cautiously hopeful. Many insects produce sounds. Probably all are sensitive to sounds and vibrations. Many species respond to artificial sounds, and many more have communication systems based on sounds. Practical controls for insects by sounds, even pilot-scale tests of practicality, remain for the future.

Work is under way to develop highly sensitive devices for perceiving and identifying the sounds of insects. It is hoped that species-specific sounds are produced frequently enough to permit the identification of insects in hidden environments such as stored grain and timbers.

BARRIERS AND EXCLUDERS

The category of barriers includes a wide variety of physical factors that can be employed to prevent insect problems and, in a few instances, to correct undesirable conditions. Generally, prevention is more desirable than correction, but it is difficult to sell, since human nature too often overlooks the desirability of the prevention approach. It is better, for example, for a housewife to put her baking flour in a jar or other protective container than to throw it away later because it has become infested with flour beetles.

MODIFIED TERRAIN

The nature of terrain can influence the success of certain insect populations either by restricting movement, or by being an undesirable environment for development. Altering the terrain has brought about the control of several insects. Ditching to remove standing water or to hasten the flow of existing waterways is a standard practice in mosquito-control operations. Wet areas are thus eliminated, and clean banks discourage successful larval development.

In a more indirect manner, ditches have been employed to control the billbug, *Sphenophorus callosa* (Olivier), in corn. The adults feed on corn; however, larval development requires sedge plants (*Cyperus esculentus* L.). Ditching dries the environment of the sedge and thus breaks the life cycle of the billbug.

Small ditches or furrows were formerly used as a barrier against migrating chinch bugs. Such a procedure was usually accompanied by a dust mulch or creosote strip. Similar procedures are still used in some areas of the world to intercept migrating armyworms, *Pseudaletia unipuncta* (Haworth), which, once trapped, are killed mechanically or with poisoned bait.

ADHESIVES

Insects are generally vulnerable to sticky surfaces on which they become attached by legs, wings, or body. Common among the adhesives are products containing a mixture of hydrogenated castor oil, natural gum resins, and vegetable wax.

Sticky surfaces have been used for the control of flea beetles in corn. Vertical sheets covered with an adhesive material were attached to cultivator frames in such a manner that they were drawn along between the corn rows just above the surface of the ground, to capture and hold the insects.

Both the spring cankerworm, *Paleacrita vernata* (Peck), and the fall cankerworm, *Alsophila pometaria* (Harris), can be greatly reduced in numbers by the use of sticky bands wrapped around the trunks of fruit and shade trees 2 to 4 feet from the ground. In the spring or fall when egg-laying takes place, the wingless females are stopped and trapped as they crawl up the tree trunks.

Another use of banded trees is that employed to protect valuable groves, plantings, and parks from periodical cicadas, *Magicicada septendecim* (Linnaeus). The cicada nymphs are trapped as they emerge from the ground and start their ascent up the tree trunks; the accumulations should be raked off daily. A similar technique is employed to trap larvae of the gypsy moth *Porthetria dispar* (Linnaeus), as they ascend trees from their daytime hiding places on the ground.

One of the oldest, and still very effective, means of reducing house fly populations in enclosures is by the use of sticky ribbons. These devices are extended from an overhead location in areas of probable fly activity; they capitalize on the behavior of the fly as it orients itself and alights on narrow, vertical objects. Such procedures do not solve the over-all fly problem of an area but do give continuing relief in limited areas.

SCREENS AND SHIELDS

Numerous materials are successfully employed, not to destroy insects, but to exclude them from being pestiferous or destructive, or to prevent them from breeding. Screening woven from cloth, metal, plastic, or fiber glass has been used for years on vents, windows, and doors of buildings to exclude the house fly, mosquito, and a multitude of other invaders. Screen doors are designed to swing out as a further assurance of exclusion of house flies; and, in some areas, a procedure—not recommended—is to hang balls of cotton on the screen, presumably to frighten the flies. Large screened enclosures are under test as an excluding device over swine waste-disposal beds.

Metal is used for subterranean termite shields around the foundations of buildings. To be at all effective, however, such shields must be extremely well installed, which, regrettably, is not often the case. Even those best installed cannot be relied on with complete confidence because of the ability of termites to tube around them or bypass them completely. In recent years, metal shields have been less frequently recommended, and persistent soil chemicals have been substituted for them.

Plastic sheet, notably polyethylene, has found its place in a number of situations where boring insects are not involved. As a liner for food packages, it is mentioned elsewhere. One of the most unusual uses has been the experimental spreading of huge sheets of the material over waste lagoons, at or near tomato-canning plants. The purpose is to prevent flies from laying eggs in the waste and to render the substrate anaerobic and thus less attractive and unsuitable as a breeding medium.

Cloth netting has a number of uses, some of which predate the turn of the twentieth century. Young fruit trees can be protected against periodical cicada attack by covering with cheesecloth, and shade or tent tobacco is secondarily protected by cloth against egg-laying activities of hornworm moths. World War II proved the value of using netting over sleeping soldiers as a protection against malaria-carrying mosquitoes; this method is still common in the tropics.

AIR AND WATER

Air and water are both highly effective natural barriers to movement of some insect populations. To manipulate air as a control measure has been only moderately successful. So-called air doors, however, have found a place in commercial establishments where permanent excluding devices are impractical because of the almost constant use of the openings. The principle involves the rapid passage of a continuous sheet of air across an opening. The use of such barriers is limited to the exclusion of flying insects, such as flies, mosquitoes, gnats, and small moths. The equipment used to generate this high-velocity air is expensive and must be properly designed and installed to be effective.

Considerable success has been realized with the use of water, both by manipulating naturally occurring bodies of it and by using it directly as a control application. The manipulation of the water-surface level for mosquito control and flooding for the control of a number of agricultural pests are discussed in Chapter 10.

The directed use of water by means of syringing involves the forceful application of it to plants. Formerly, this method was widely practiced to prevent build-up and to reduce existing populations of mites and mealybugs on house plants, shrubs, and small trees. Syringing of roses in greenhouses was standard practice but has generally been discontinued because it promoted the development of black spot and other plant diseases. The method, however, is still the salvation of many housewives who experience minor pest problems on their flowers and houseplants.

Other applications of water, employing somewhat different principles, include submerging cut logs to minimize wood borer damage and washing woolens before storing to decrease their acceptance to freshly hatched larvae of clothes moths.

PROTECTIVE PACKAGING

Insect infestation of packaged dry foods is a serious problem confronting the food industry. More than 50 species of insects attack dry, processed plant products used for human foods and animal feeds. These insects are capable of infesting the product during processing, while it is in storage, in transit, on the retailer's shelf, or even while in the possession of the consumer. Regardless of where and how the infestation occurs, in the eyes of the customer it is the manufacturer who is responsible for the condition of his product until it is ultimately used. As a rule, the only feasible way the manufacturer can protect his product against insect infestation is by using insect-resistant containers.

Tightly sealed glass and rigid metal containers are naturally insect-resistant, but the textile, paper, fiberboard, foil, and plastic-film (flexible) containers are not. A large percentage of dry foods are packaged in containers that provide little or no protection against insect infestation.

The success of a food container as an excluder depends on the packaging material used, the construction of the container, and the tightness of the closures. The ideal insect-resistant package is made of material that is naturally resistant or chemically treated to resist insect penetration, and structurally designed and fabricated to prevent insect invasion.

Although all flexible-type packaging materials can be penetrated by certain species of insects, such as the cadelle, the lesser grain borer, and the cigarette bettle, *Lasioderma serricorne* (Fabricius), some packaging materials have greater inherent resistance than others to penetration. For example, certain flexible films, such as polycarbonates, have greater resistance than polyethylenes, and fiberboard is more resistant than kraft paper to insect penetration. Therefore, consideration should be given to the most insect-resistant packaging material suitable for the type of package and commodity involved. Furthermore, one packaging material can be utilized to supplement another. For instance, it may be possible to use laminates with the most resistant materials on the outer surface of the package. For economic reasons, some of the susceptible packaging materials have to be used for certain food packages. The only recourse that can be taken is the use of a repellent on the outer surface to prevent insect penetration. This type of approach is used with kraft-paper multiwall bags. The outer ply is coated with a pyrethrins–piperonyl butoxide formulation, and this treatment in combination with insect-tight closures and a longitudinal seam provides excellent protection against insect infestation for 9 to 12 months.

Insect-tight construction of food packages is imperative for preventing insect infestation. This principle applies to all types of packages, whether the container is a bag, a carton, or a pouch. There must be no open joints or corners. For bags, tape-over-stitch or pasted-open-mouth closures with the continuous glue lines right up to the edge of the top or closure flap are the most effective. The flaps on cartons or boxes must overlap, and there must be a continuous glue line around the entire periphery of the closure if insects are to be kept out of the container. Overwraps using the more resistant films with continuous seal lines along all edges of the film are also very effective in making a container structurally insect-tight. At the present time, no repellent treatments are recommended for use on unit food packages.

In a different sense, packaging can be used for temporary protection, as in the storage of woolens and furs. Such items can be wrapped with heavy paper or flexible films and tied or sealed to prevent fabric pests from gaining entrance.

TYING

A handy method for reducing corn earworm damage in small plantings of sweet corn is to tie the husk tightly to the developing ear about an inch below the tip of the cob. A stout twine wrapped twice around the ear and fastened with an easy-to-tie nonslip knot, such as the clove hitch, will usually confine the earworm and the damage to the ear tip. The twine should be applied before the young larvae migrate down the ear from the silks where the eggs were laid. The developing ear becomes grooved by the tight twine, and the tip is easily removed.

ELECTRICAL BARRIERS

Electric screens have been used for many years on doors and windows to exclude flies and other insects from restaurants, hospitals, receiving rooms of grocery stores, food kitchens, and barns. They are designed to operate on 110 to 120-V, 60-cycle alternating current.

Electric barriers are also used in laboratories to confine insects in their rearing containers. A common method of constructing this barrier is to apply a strip of aluminum foil to a double-adhesive-faced tape and fasten this tape to the inside wall of the metal container near the top. The foil is attached to one terminal of a "B" battery, and the container is attached to the other terminal. Some thought has been given to a modification of this technique for the exclusion of migrating insects and other arthropods entering buildings or crossing fields.

MECHANICAL METHODS

The control of insects by mechanical methods is based on the principles of removal and direct destruction. Some advantages of these methods are that they utilize home labor, equipment costs are low, and they pose no residue problems. However, the methods are rarely highly efficient and often require frequent or continuous use. Furthermore, hand labor, which was their greatest asset, has become so costly in some areas of the world that mechanical control has become less feasible.

HANDPICKING

Undoubtedly the first use of this method was for collecting insects as food. The earliest use of it as a prescribed control procedure may have originated as a means of controlling hornworms, since it was extensively used by American pioneers to protect tobacco and tomatoes from these pests. At the turn of the twentieth century, many cotton farmers tried to control the boll weevil by handpicking and destroying fallen infested squares. Handpicking of adults and egg masses was "the method" for combating the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), 100 years ago, but even then many farmers complained that the effort was futile, because, with continuous reinfestation, daily collection was necessary, and on large fields this was impractical, if not impossible. At present, high wages make the cost prohibitive in many places. In some developing countries, handpicking of egg masses, adults, and large larvae of many pests, notably pentatomids, chrysomelids, sphingids, noctuids, meloids, and scarabids, is frequently practiced. The size of the field, rapidity of reinfestation, and availability or abundance of cheap labor all interact to determine the effectiveness and practicality of the method. The handpicking of tomato hornworms in small home gardens, or of bagworms, *Thyridopteryx ephemeraeformis* (Haworth), on a few ornamental shrubs, is often a fully adequate and recommended practice.

JARRING AND SHAKING

There are many variations in the jarring and shaking technique, which some say originated from a farmer's casual observation that the fruit on an isolated plum tree growing out of a creek bank and leaning over the water was relatively free of plum curculio damage. The farmer concluded that the wind caused the adult insects to drop into the water and be carried away. Fruit growers then discovered that by placing sheets under the tree and jarring the tree, they could collect and destroy the adults before they could deposit their eggs. This method and a variation involving the use of inverted umbrellas became common, and for many years the practice was recommended for plum curculio control. In some cases, farmers confined flocks of poultry in the orchard to pick up the insects as they were jarred or accidentally dropped to the ground. Jarring is still used to determine curculio abundance and to time spray applications, but the inefficiency of the method, as well as labor costs, precludes its use as a control measure in many areas of the world.

Variations of the method involving hand shaking, flailing with brush, and dragging ropes to dislodge a variety of pests on grain, vegetable, and forage crops were once used extensively and are still practiced in areas where labor is cheap. These practices are usually used in conjunction with some other means of control, for example, hand beating Colorado potato beetle larvae into buckets containing a water and kerosene mixture. In the 1920's, some cotton farmers hung gunny sacks on their cultivators so that as they were dragged over the cotton plants insect-infested squares would be dislodged and drop to the ground, where the sun and hot soil would destroy the insects. About the same time, a hand-carried mechanical contraption utilizing wooden paddles or bars was placed on the market to knock fleahoppers, aphids, thrips, and boll weevils to the ground or into pans of oil.

DRIVING AND HERDING

Man has at times attempted to protect his crops by driving away his pests (birds and mammals as well as insects). When the locust hordes appeared, the natives used smoke in various ways, beat drums, blew whistles, screamed, sang, and, by every method they could think of, tried to scare the pests away. People marching to and fro while maintaining an oblique line or pattern at all times during the march herded the locusts out of the field. This practice was frequently used in the United States during the late nineteenth century to protect crops from grasshoppers and Mormon crickets, *Anabrus simplex* Haldeman. It was observed in Iowa and Illinois as late as 1930 and may still be used occasionally to minimize grasshopper damage on valuable vegetable crops when spraying or baiting might be considered objectionable. Herding has also been used to drive blister beetles, *Epicauta* spp., from fields.

COLLECTING DEVICES

Various collecting devices, ranging from a bucket and a paddle to large custom-made horse-drawn machines typified by the "hopperdozers," were used extensively for grasshopper control in the Great Plains area of the United States in the latter half of the nineteenth century (Figure 32). Even during the depression years of the 1930's, some farmers resorted to the use of hopperdozers, but on most farms their use gave inadequate control compared with the poison bran bait method then in common use. Even against the vulnerable nymphs, hopper-

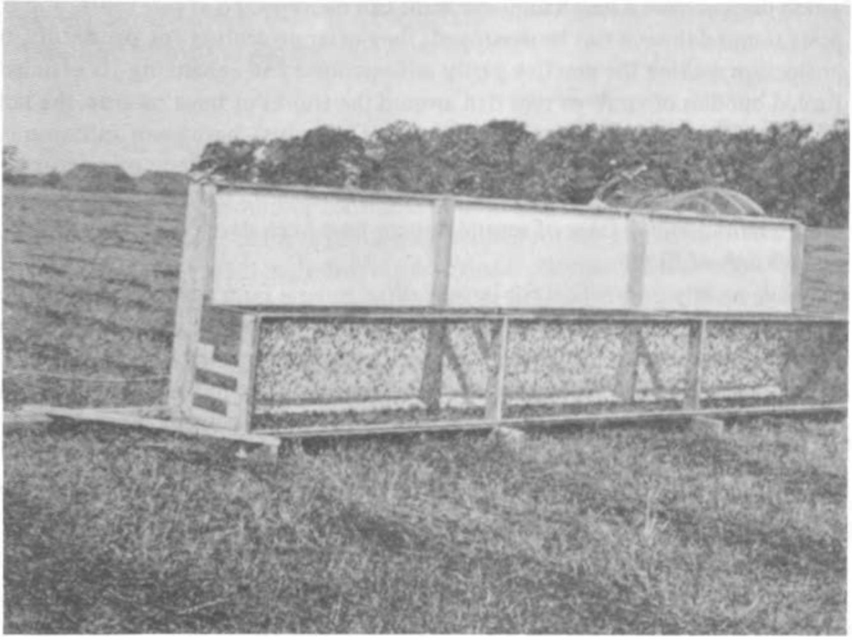

FIGURE 32 Hopperdozer used in the Great Plains in 1919 for grasshopper control.

dozers were unable to remove more than two thirds to three quarters of the population present.

In parts of the Near East, Asia, and Africa, various types of hand equipment, e.g., insect nets, baskets, and blankets (carried by two people), have been used, and in some remote areas are still used, to collect locust nymphs and adults.

In earlier days, grasshoppers and locusts collected in hopperdozers or devices were eaten by man or fed to livestock; thus there was an added incentive for using the method.

Other devices often referred to as insect collectors, which have been used in conjunction with light traps, electric grids, and baited or other traps, are discussed elsewhere.

TRAPPING

Over the years, a great variety of devices or techniques have been developed for catching or trapping insects. Boards, strips of bark, bundles of grass, and pieces of leather or cloth laid on the ground near plants to be protected are examples.

These devices have a dual value: the traps can be inspected at intervals, and the pests trapped therein can be destroyed; they offer protection for predators, the protection making the practice partly self-operative and enhancing its efficiency. Rolled bundles of straw or rags tied around the trunks of trees to trap the larvae of the codling moth, *Carpocapsa pomonella* (Linnaeus), have been in common use for 100 years. More recently, chemically treated bands made of corrugated paper, which kill as well as trap the larvae, have replaced the more primitive bands. Baited screen traps of several designs have been developed to entrap many kinds of flies.

While mostly impractical for large-scale or general farm pest-control efforts, traps are still helpful in controlling insects such as the squash bug, *Anasa tristis* (De Geer), and cutworms in home gardens, and, when properly used, baited-screen fly traps still catch quantities of different flies around places of business and the home. In discussing trapping, mention must be made of jugging for bumble bees. An opaque jug is half-filled with water and placed near the nest entrance; when the bees leaving or entering the nest hear their wing vibrations over the jug, they are attracted and are drowned.

BRUSHING AND SWEEPING

Brushing of blankets and woolens, combined with airing and sunning, was once a principal method of controlling clothes moths and carpet beetles, and is still used as a major or supplemental method by many housewives. Sweeping and vacuuming are also at least partially effective in reducing these insects and a number of other household pests, such as boxelder bugs, *Leptocoris trivittatus* (Say), and brown dog ticks, *Rhipicephalus sanguineus* (Latreille). Frequent sweeping or vacuuming in granaries, feed mills, flour mills, and similar plants is an essential part of a good insect-control program. The practice of brushing, currying, and combing has long been a common means of reducing lice, ticks, and fleas on pets and livestock. A modification of this method is the use of a net with long strings draped over horses; the movement of the strings brushes away annoying flies.

WORMING

Until well after the turn of the twentieth century, textbooks strongly recommended the use of a knife or bent wire as one of the best methods for controlling borers in woody plants, and the method is still practical where only a few trees or plants are involved and labor costs are not a major factor. In many parts of the world it remains the basic means of borer control in shade and fruit trees. In India and most other areas where coconuts are grown commercially, expert climbers have become specialists in thus removing rhinoceros beetles from the crowns of the coconut palm trees.

SWATTING AND CRUSHING

The flyswatter method of control is of doubtful value where large fly populations are involved but is highly recommended for the elimination of a few stray flies. It is also useful in destroying occasional cockroaches, boxelder bugs, mosquitoes, and other household pests. Although this method leaves stains where insects are crushed, it leaves no toxic residue.

Several methods that involve crushing have been used at one time or another. When armyworms, crickets, chinch bugs, or immature grasshoopers were found moving from one field to another, farmers drove back and forth using rollers or plank drags to crush the pests. The machinery used in modern cotton gins is highly effective in killing pink bollworms.

SIFTING AND SEPARATION

The sifting of flour to remove insects has long been a common practice, and farmers frequently run grain over a screen while moving it from one bin to another. In the early 1940's, the U.S. Commodity Credit Corporation screened millions of bushels of grain to reduce insect infestation and remove the cracked grain and meal responsible for maintaining high populations of flour beetles.

Sifting has reached a high degree of sophistication in recent years in the industrial processing of grain. Modern mills incorporate a series of sifters, floating devices, and separators to obtain meal and flour products free of insect contaminants.

MACHINERY

Several pieces of farm machinery have been designed partly or entirely for destroying insect pests. Shredding machines were constructed or modified to increase their effectiveness in destroying pink bollworms, European corn borers, and many other pests found in crop refuse. The inventors had white grubs and other subterranean insect pests in mind when they developed rototillers and soil pulverizers. It is doubtful that use of these machines can be justified on the basis of insect control alone, but, when the equipment is used for tillage, it does destroy large numbers of soil insects. Harvesting cotton with the modern mechanical strippers removes all the bolls from the plant, thus assuring the grower that all infested bolls will go to the gin and be subjected to crushing during the ginning process. The development of mechanical pickers for fruits and vegetables may not have insect control as one of the objectives, but the side benefits in that regard could be considerable. For example, there is a definite indication that single-run mechanical picking of tomatoes will reduce the *Drosophila* sp. problem by harvesting principally uncracked and uncrushed fruit, which is moved rapidly to the processing plant. The residue of crushed fruit left in the field, however, must be viewed as a potential breeding reservoir for nearby fields.

Although never recommended by state or federal agencies, a tractor-mounted suction machine, which reportedly sucked thousands of insect pests into bags where they could be destroyed, was widely advertised and sold in parts of Texas and adjacent cotton-growing areas.

One of the most recent attempts to develop farm machinery specifically for insect control has been the attempt to develop a flail machine for cotton-insect control. Pink bollworms can be greatly reduced by shredding cotton stalks by the impact of the flail. In the experimental stage is a three-unit flail machine, complete with air blower, designed to collect and destroy fallen cotton squares, thus reducing larval and adult populations of the boll weevil. In some fields the machine destroyed 85% of the infested fallen squares (Figure 33).

Specially developed machinery is being used for mechanical insect control in grain-processing mills. One successful device is called the Entoleter; it employs centrifugal force to break kernels infested or damaged by insects. This equipment kills all stages of insects, pulverizes broken grain, and passes the whole kernels without injury to them. Flour mills utilizing this type of equipment produce flour products relatively free from insect contamination.

WASHING, CLEANING, AND SOAKING

Washing with warm soapy water to control aphids, whiteflies, and mites on house plants is still a common and useful practice, although most uses of this technique are no longer generally pursued. There are principles to be found in once-recommended techniques, such as use of these methods to induce the eggs of the horse bot fly, *Gasterophilus intestinalis* (De Geer), to hatch and then to remove the larvae; the delousing of soldiers' clothing in World War I; and the application of scalding water to flush out and kill bed bugs in crevices of walls and beds.

Clothes moths and carpet beetles will attack clean wool, but they prefer and develop better on wool soiled with perspiration, urine, and food. Garments that

FIGURE 33 **Flail machine designed to collect and destroy fallen cotton squares for boll weevil control.**

are washed or dry-cleaned before storage are less attractive to fabric insects, and the laundering will kill any insects on the clothing.

SEMIMECHANICAL PRACTICES

Burning, plowing, the spreading of manure, and several other practices at times referred to as mechanical are closely related to cultural control and are discussed in Chapter 10.

ATMOSPHERE AND ATOMS

A relatively new approach to physical control is the manipulation of the environmental atmosphere of specific insects. Carbon dioxide (CO_2) has long been employed to immobilize test insects used in bioassay, and its use in insect control has often been contemplated. Some success has been obtained in laboratory experiments using this molecule to produce mortality in larval populations of the red flour beetle, the Indian-meal moth, *Plodia interpunctella* (Hübner), and dermestids. The successful technique of burying fruit containing the larvae of Mexican fruit flies, *Anastrepha ludens* (Loew), in order to destroy the infestation is attributable to an increased atmosphere of CO_2. Exposures of insects to an atmosphere composed entirely of carbon dioxide generally cause death after 12 to 24 hours. A similar technique utilizing a high nitrogen atmosphere can produce death in an even shorter time.

Such techniques could have the advantage of controlling stored-product insects without creating hazardous residues. Tight storage would seem most appropriate, but the possibility exists that continuous release of CO_2 or nitrogen in controlled amounts could produce and maintain a lethal atmosphere.

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CHAPTER 12

Antimetabolites, Feeding Deterrents, and Hormones

Among the numerous potential approaches to insect control is the utilization of several unrelated groups of chemical agents, not otherwise used, that offer considerable promise for the control of insects by disrupting their nutritional and developmental processes. Certain antimetabolites disrupt the normal processes of assimilation essential to the growth and development of insects. In addition to the repellents, which are discussed in Chapter 14, there are feeding deterrents that interfere with the ingestion of food. Some hormones and hormone-mimicking compounds also prevent normal development by interfering with the phenomena associated with molting and other endocrine-mediated processes.

ANTIMETABOLITES

Antimetabolites are substances that inhibit the utilization of metabolites, usually by antagonistic action. They chemically resemble essential nutrients and, when introduced into a biological system, prevent the nutrients in food sources from performing their normal function. Selected antimetabolites act as "metabolic disruptors."

Most antimetabolites are low in mammalian toxicity and are probably safe for use in pest control. When chemicals of this nature are used for insect-proofing of fabrics, minute amounts are ingested by fiber-feeding insects, which soon exhibit symptoms of dietary deficiency, as indicated by body-weight losses and early death. The insects quickly discontinue feeding, and losses in weight of the fiber are held below tolerances allowed under recognized standards.

Some antimetabolites are capable of inhibiting two or more metabolites. A precursor might be effected that normally gives rise to two or more nutrients. This appears to occur with the histamine antimetabolite imidazole. Addition of histamine, or its salts, completely reverses the action. Niacin acts in a related manner. The precise selectivity of action is not clear, but it appears that imidazole is antagonistic to both histamine and niacin.

The principal advantage of some antimetabolites for pest control is their safety, and the major disadvantage is the restricted area of usefulness. Some antimetabolites are highly effective when added to the diet of pests that have no access to untreated food; they would, however, have only limited value where polyphagous insects are concerned.

Continued research with antimetabolites for insect-pest control is needed. Some aspects particularly worthy of further investigation are: (1) the search for new antimetabolites that affect different physiological processes in insects, especially those occurring in insects and not in other groups of organisms, such as vertebrates; (2) the synergistic effect attained by using combinations of similar or unrelated antimetabolites; (3) the effect of trace nutrients in relation to both the biosynthetic and the ingestion processes; and (4) the effect of antimetabolites or antibiotics on the balance and the imbalance of metabolites produced in symbiotic relationships between insects and their associated microorganisms. Additional information in these areas may greatly extend the use of these potent chemicals in economic entomology.

FEEDING DETERRENTS

The ultimate goal in insect-pest control is the protection of the crop or other commodity from damage by the pest concerned. Classically, this has been accomplished by the elimination of the pest by a variety of means—trapping, poisoning, driving it away with repellents, or keeping it away with barriers. Feeding deterrents accomplish this goal of protection by preventing the feeding of the pest, thus eliminating the damage rather than the pest. Strong feeding deterrents may also eliminate the insect by starvation, especially in oligophagous species.

The best example of a feeding deterrent, and the only one tested on a large scale, is the synthetic compound 4′-(dimethyltriazeno)-acetanilide. This material was effective in field tests when applied to surfaces on which the insect pests ordinarily feed. Fair to excellent results were obtained against such surface-feeding insects as the cabbage looper, *Trichoplusia ni* (Hübner), cabbageworms, *Pieris* spp., the cotton leafworm, *Alabama argillacea* (Hübner), hornworms, *Manduca* spp., the boll weevil, *Anthonomus grandis* Boheman, and cucumber beetles, *Diabrotica* spp.

No control was obtained when certain insect larvae fed under the treated surfaces, for example, the corn earworm, *Heliothis zea* (Boddie), bollworms, *Heliothis* spp., the pink bollworm, *Pectinophora gossypiella* (Saunders), the codling moth, *Carpocapsa pomonella* (Linnaeus), and cabbageworms (inside the cabbage heads). The same insects, however, were controlled in an earlier stage when they fed on the surface. Corn earworms would not feed on treated corn leaves in laboratory tests. They also would not feed on treated exposed silks of corn, *Zea mays* Linnaeus, in the field, although they fed readily on the untreated silks deeper in the ear.

Fabric, paper, or cardboard impregnated with the chemical was protected from the attack of penetrating or chewing insects, such as the black carpet beetle, *Attagenus piceus* (Olivier), larvae of the webbing clothes moth, *Tineola bisselliella* (Hummel), and the lesser grain borer, *Rhyzopertha dominica* (Fabricius). However, pests that feed on plants or animals by piercing and sucking, such as aphids, leafhoppers, ticks, mosquitoes, and biting flies, were not controlled by such treatment. Another synthetic, triphenyltin hydroxide, and certain other tin compounds, have been reported to protect against damage by clothes moth larvae and other caterpillars.

Several naturally occurring materials extracted from plants and chemically identified have shown a strong feeding deterrency to a number of insects. Examples of these deterrents are 6-methoxybenzoxazolinone from corn for larvae of the European corn borer, *Ostrinia nubilalis* (Hübner); a number of alkoglycosides (demissine, dihydro-*a*-solanin, leptines, solacaulin, solanin, and tomatin) from various species of Solanum for the Colorado potato beetle, *Leptinotarsa decemlineata* (Say); and coumarin (in high concentrations) from sweetclover for the vegetable weevil, *Listroderes costirostris obliquus* (Klug). Strong feeding deterrents to the boll weevil are present in calyxes of *Hibiscus syriacus* Linnaeus (Rose of Sharon) and in tung oil and meal. They appear to be glycosidic in nature but have not been chemically identified. These examples indicate that the area of naturally occurring feeding deterrents to insects in plants offers a fruitful field for research. The utilization of these feeding deterrents as a future or adjunct method of insect control will depend largely on the speed of chemical isolation and identification. The role of naturally occurring feeding deterrents in host-plant resistance is discussed in Chapter 6.

Feeding deterrents have some advantages over the conventional methods of pest control, particularly in integrated control programs. The only insects likely to be affected by feeding deterrents are those that attack the crop being protected. Parasites and predators of the pest are not harmed, and, since the target organisms are not killed, the beneficial insects can thrive on them. This contrasts with the use of an insecticide, which often kills the parasites and predators and most of their food supply. Finally, the known feeding deterrents have rather low mammalian toxicity; the acute oral LD_{50} of 4′-(dimethyltriazeno)-acetanilide to rats is 510 mg/kg, and most of the other synthetic feeding deterrents have similar low toxicities.

Feeding deterrents also have certain disadvantages. Those now known have a limited spectrum of activity, being effective only against chewing insects, and then only against surface feeders. The entire surface of a plant or part to be protected must be covered. Areas of poor coverage were badly damaged in tests of grapevines for control of the Japanese beetle, *Popillia japonica* Newman, and new growth was attacked as soon as it appeared, because it was not protected. To overcome the shortcomings, a material would need systemic properties, so that it might be translocated to new growth and to areas of poor coverage. Such systemic materials might also be effective against the large number of economically important sucking, piercing, or penetrating insects. Future research will undoubtedly be focused on such needs.

HORMONES

The process of molting, including the related phenomena that are characteristic features of growth, maturation, and metamorphosis in insects, is regulated by hormones. There are three important kinds of hormones that mediate the process: the brain hormone, the ecdysones (molting hormones), and the juvenile hormone. Three insect ecdysones have been isolated and chemically identified, and several similar or related steroids with molting hormone activity occur in high titer in certain plants. Only one of the insect ecdysones, *a*-ecdysone, has been synthesized. A structure has also recently been reported for the Cecropia juvenile hormone, and its synthesis should be forthcoming in the very near future. In addition, for several years we have had chemical compounds available that exhibit many of the biological activities of the natural juvenile hormone. These compounds, which have been designated juvenile-hormone mimics, include the sesquiterpenes, farnesol, farnesenic acid, and certain of their derivatives. Several of these compounds are highly active at nanogram (10^{-9} g) levels and penetrate the insect cuticle, as does the natural juvenile hormone. Because of these characteristics, their ready availability, and knowledge accumulated through laboratory experimentation, the juvenile hormone and its mimics offer the greatest immediate potential as insect control agents.

The molting process in insects is brought about by the molting hormones, whether the molt be from larva to larva, larva to pupa, or pupa to adult. However, in a larva-to-larva molt, in which the insect retains certain immature characteristics, the juvenile hormone is also present. Thus, the juvenile hormone permits growth but not maturation. One possible use in control would be to bring materials with juvenile-hormone activity in contact with insects either in the last nymphal instar or in the pupal stage, at which time the juvenile hormone is not normally present. This would result in the retention of immature characteristics and cause the production of an intermediate form, thus inhibiting normal development. For instance, when nanogram quantities of some of the more potent juvenile hormone-mimicking compounds are brought into contact with the cuticle of a pupa of the yellow mealworm, *Tenebrio molitor* Linnaeus, the insect will molt either to a second pupa, which will not develop further, or to an adult which retains certain pupal characteristics. The malformed adult either fails to emerge from the pupal case or retains the pupal genitalia and is unable to reproduce (Figure 34).

Certain compounds with juvenile-hormone activity have gonadotropic (ovarian-maturation) hormone activity and might have potential use in control

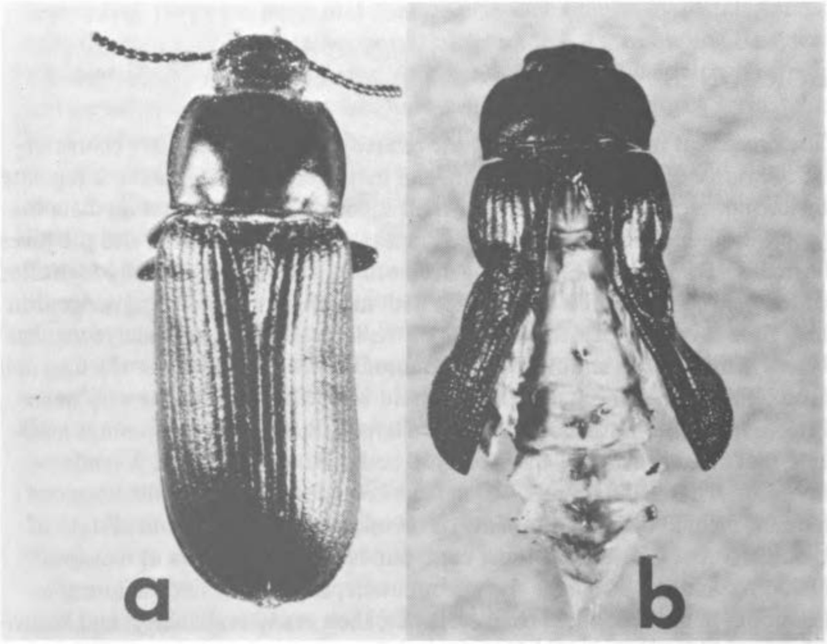

FIGURE 34 Normal (a) and juvenilized (b) adults of the yellow mealworm, *Tenebrio molitor* Linnaeus. Juvenilized insect is from a pupa treated topically with submicrogram quantities of the juvenile hormone-mimicking compound *trans, trans* 10,11-epoxyfarnesenic acid methyl ester. This insect has retained a number of pupal structures, including the pupal genitalia. The pupal exuviae were removed, since normal eclosion could not occur. (USDA photograph)

by stimulating ovarian development in insects undergoing adult diapause or aestivation. In these insects the cessation of ovarian development and hypertrophy of the fat body are salient physiological changes, which also occur in certain nondiapausing adult insects that have been deprived of the gonadotropic hormone by removal of the corpus allatum. The untimely reinitiation of ovarian cycles and the concurrent interruption of the biochemical and physiological quiescence in such insects during unfavorable environmental conditions could result in destruction of the insect.

One possible advantage of the juvenile hormone and its mimics is that those compounds that have hormone activity in insects have not been structurally related to any of the known vertebrate hormones. However, pharmacological and toxicological tests will be necessary to determine what hazards, if any, these compounds present to man and other vertebrates and to plant life. Another possible advantage is that certain of the juvenile-hormone mimics have shown considerable specificity as to the insect species they affect; this would be an important factor in selective control.

A disadvantage of mimicking compounds is that many of those tested have little effect on larval development. Consequently, it would be necessary to use either repeated applications or compounds with considerable persistence to assure contact with the last larval or nymphal stage, or the pupal stage, of the insect. Many of the presently available compounds would not protect against the damage caused by larval or nymphal stages, which for many species are the most destructive. However, this disadvantage may be largely obviated in the future by an increased knowledge of the action of the juvenile hormone and mimics. The recent report that a naturally occurring juvenile-hormone mimic also has ovicidal activity substantiates this probability.

Important research needs in the use of insect hormones as chemical control agents include: (1) more thorough testing of the known active compounds on a wider spectrum of insects in relation to the known morphological effects and for the detection of more subtle physiological and biochemical effects; (2) an intensified synthesis and testing program, with considerable effort given to relating structure to hormonal activity; (3) the development of new or improved assays for evaluating compounds with hormonal activity and their analogues, and related compounds which might have antihormone or antagonistic activity; and (4) a program aimed at detecting and then isolating and identifying the compounds with juvenile- or molting-hormone activity present in plants and determining the roles these substances play in protecting plants from insect attack. Finally, the availability of the insect ecdysones and related steroids with molting-hormone activity, both synthetic and of plant origin, should stimulate research on these hormones and certain of their structural analogues for both their positive and negative effects, to determine how these important hormones may be used in insect control.

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CHAPTER 13

Chemical Attractants and Insect Behavior

Chemical attractants and associated agents, such as stimulants and arrestants, have been widely used for many years in studies of insect behavior. They have served many useful purposes as lures in traps, for example: (1) to sample insect populations to determine their relative densities from time to time and from place to place, (2) to trace the movement of marked insects in dispersion and migration studies, (3) to study survival of insects in their natural environments, and (4) to study behavior associated with the search for mates, food, and oviposition sites. Attractants and associated agents have also played an important part in the control of some species. Here again, as lures in traps, they have served to detect the presence of pest infestations, delimit their extent, and indicate where and when their intensity was great enough to require control measures. Sometimes the traps alone have destroyed enough insects to be a factor in control. More often, the direct usefulness of these agents in insect destruction has been achieved through their incorporation into poison baits.

Entomologists are searching for more selective methods of insect control—methods that will exert their effect only on the target species and on other species that depend directly on the target species for their existence. Because chemical attractants and the related agents affecting insect behavior are often quite specific, they are likely to provide such selective weapons. With these agents, the target species can be brought into contact with toxicants, sterilants, pathogens, or mechanical devices exposed in ways that do not contaminate or harm the general environment or endanger other species. Some behavioral control agents are physical (sound or electromagnetic radiations); these are discussed in Chapter 11. Agents influencing insect behavior have not been exploited as fully as most control agents; therefore, they provide a particularly promising field for additional research.

CHEMICAL ATTRACTANTS

Attractants constitute a particularly fruitful field for research because they play a dominant role in the most vital aspects of insect behavior. They govern the activity of insects in seeking food, mates, oviposition sites, and sometimes the protected places where they pass the inactive stages of their development. Pests of both plants and animals, as well as saprophytic species, respond to attractants in their search for food. Some chemical attractants, especially those associated with sexual behavior, are biologically active in almost incredibly small quantities; e.g., 10^{-7} μg of the pheromone produced by the female gypsy moth, *Porthetria dispar* (Linnaeus), will attract male gypsy moths in the field.

Attractants, in the strictest sense, are chemicals or other stimuli that cause insects to make oriented movements toward the source. Almost as important as the attractants, and often confused with them, are the arrestants and locomotor, feeding, mating, and oviposition stimulants. The entire behavioral pattern of feeding, mating, or ovipositing may involve a number of stimuli. Such a pattern begins when an insect that has been in a quiescent state enters a physiological condition in which it is ready to seek food, a mate, or a place to oviposit. A locomotor stimulant, either from within or outside the insect, may cause it to begin unoriented searching movements; an attractant may cause these movements to become oriented; an arrestant may cause them to cease when the food, mate, or oviposition site has been reached; and a feeding, mating, or oviposition stimulant may induce the insect to initiate the consummatory action. A single stimulus may function in all these ways, or the entire behavioral pattern may result from a sequence of different stimuli. The stimuli may be chemicals, sounds, other vibrations or movements, or electromagnetic radiations. Biorhythm phenomena triggered by light or other stimuli may be involved in the various sequences.

LOCOMOTOR STIMULANTS

The locomotor stimulant initiates searching but need not in itself cause oriented movements. Light of a specific intensity or wave length may serve as a locomotor stimulant once the insect has achieved the necessary physiological condition. For example, a crepuscular species may begin a searching flight at a certain stage of twilight, but its flight is not necessarily oriented toward a light source. Carbon dioxide probably functions in large part as a locomotor stimulant in the host-seeking activity of mosquitoes, inducing increased activity but not always causing orientation toward its source. The sex pheromone of the female American cockroach, *Periplaneta americana* (Linnaeus), functions spectacularly as a locomotor stimulant for the males but is not restricted to this function.

TRUE ATTRACTANTS

Once searching movements of an insect begin, orientation may be induced by anemotaxis, chemicals, radiations, or their combinations. These may govern the search from the start. However, the initial searching may be entirely at random or only generally directed with respect to the air currents; eventually, the insect may enter the zone of activity of a true attractant, at which time its movements become oriented toward the source, to which it then proceeds by directed locomotion. An agent can properly be termed an "attractant" only if it operates to draw (or guide) the insects to the source from some distance, however short. Chemical attractants are sometimes credited with "attracting" insects for a distance of several miles, often on the basis of insufficient evidence. The mere recapture of a group of insects at the site of an attractant situated several miles from the point of release does not constitute evidence that the insects were "attracted" for the entire distance. They might have scattered at random from the site of release, or flown upwind for a part of the distance, under no influence but positive anemotaxis, before they entered the effective range of the attractant. Even the demonstration that a significantly greater number are caught with than without an attractant only proves that the insects entered the influence of the attractant somewhere along their flight paths. To prove that a chemical acts as an attractant at *X* yards from its source, it is necessary to show that the number of insects making oriented movements toward that source while they are still *X* yards from the source is significantly greater when the attractant is exposed than when it is not.

The mechanism of orientation is relatively simple with attractive radiations such as light, but with the chemical attractants, which must be volatile and airborne, the mechanism is complex and still undetermined. Some investigators still accept the theory that insects can detect and follow minute differences in a concentration gradient of the chemical in the air. Most workers, however, are convinced that attractants act by reducing the frequency of turning or inducing more positive anemotaxis, or both.

ARRESTANTS

Arrestants are agents that cause the insects to cease locomotion. They are often confused with attractants because they cause insects to aggregate on them. Sugar, for example, is frequently called an attractant for the house fly, *Musca domestica* Linnaeus, but it is nonvolatile and has no orienting action *per se,* although sugar and flies, as part of a white:black pattern, may function as a visual attractant. Flies find the sugar by random movement and cease locomotion on contact with it. This results in greater accumulations of flies on open dishes of sugar than on dishes of less active arrestants. An arrestant for the boll weevil, *Anthonomus grandis* Boheman, has been extracted from the cotton plant.

An attractant cannot be distinguished from an arrestant by means of an experiment in which the insects have a reversible choice. If, for example, three materials, *A*, *B*, and *C*, are exposed in open dishes, where insects may pass back and forth between them, a significantly greater number of insects congregated on *A* does not necessarily indicate that *A* is an attractant; it may be an arrestant. The aggregation of insects on *A* might not have resulted from oriented movement. The insects might have initially been distributed randomly and those that first reached *B* or *C* then continued random movement but those that reached *A* remained in contact with it. However, in another type of experiment the two stimuli can be differentiated. If *A*, *B*, and *C* are exposed in traps, so that the insects that enter cannot leave, a significantly greater number of insects in the trap with *A* indicates that it is an attractant, since only oriented movement to *A* would overcome the random distribution of "first choices" to a statistically significant degree.

FEEDING, MATING, AND OVIPOSITION STIMULANTS

The stimuli that cause insects to actually feed, copulate, or oviposit may but need not be the same as the attractants or arrestants. Adenosine triphosphate stimulates feeding by mosquitoes; it is not an attractant but may be an arrestant. The same is true for an unidentified feeding stimulant for the boll weevil and one for adults of the western and northern corn rootworms, *Diabrotica virgifera* LeConte and *D. longicornis* (Say) and for various feeding stimulants of house flies (Figure 35).

TYPES OF ACTIVITIES

In all insect activities elicited by chemical agents there are two elements: the reception of a stimulus and the response to it. A response to a stimulus implies

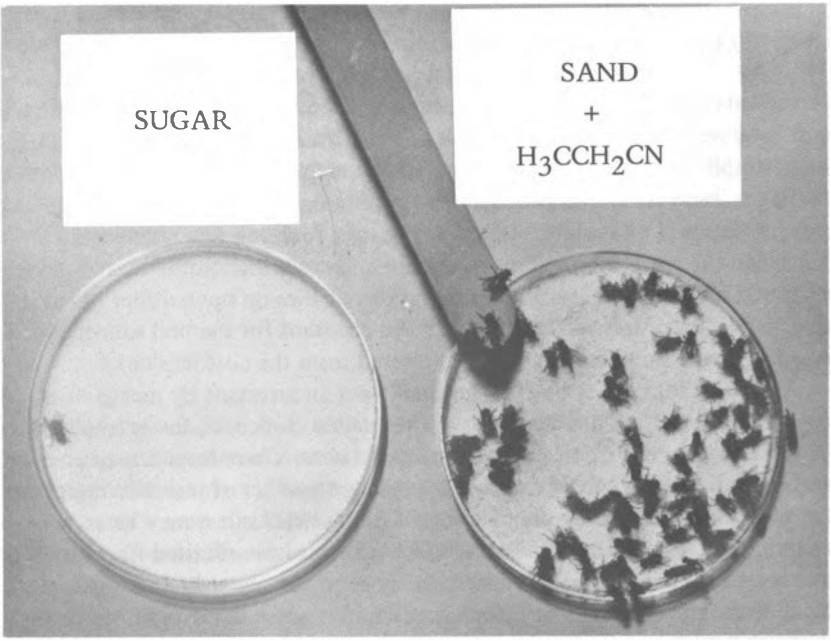


FIGURE 35. House flies gather in larger numbers on white sand treated with propionitrile, an arrestant and feeding stimulant, than on granulated sugar, a less preferred arrestant. Flies are not driven away from the chemical even when poked with a tongue depressor. (USDA photograph)

that it has been received, but reception is not necessarily followed by response. Responses may be glandular, involving the release of a secretion such as the honeydew of aphids; postural, resulting in movement of appendages or changes in the attitude of the body in any plane; or locomotory, introducing a translational movement of the insect by crawling, walking, swimming, jumping, or flying.

Responses built into the makeup of an insect and inherited from previous generations are said to be instinctive and are made regardless of previous experience of the stimulus. For such responses, the stimulus is often internal and brought about by the physiological condition of the insect. Such responses appear to be spontaneous. Responses may also be modified through experience or learning, but such modifications are seldom used in pest control, and knowledge of them is limited.

Because the main concern in work with insect attractants and related agents has to do with chemicals airborne in the vapor phase, the olfactory sense of the insect is of greatest importance. Activity in response to locomotor stimulants and attractants usually results from smell, but the remarkable sensitivity of insects to air movement is also important. Chemical arrestants, and stimulants for feeding, mating, and oviposition, commonly operate through the other chemical senses. Other types of arrestants and stimulants may act through visual, thermal, or mechanical stimuli. The precise quantitative and qualitative limits of sensitivity of receptors are known for only some senses and for very few insect species.

FEEDING

Before an insect can feed, it has to find and identify its food. For larvae this is commonly accomplished by the female parent, which oviposits on food material suitable for the offspring, even though her own food may be entirely different (see discussion of oviposition). The search for food may be initiated by a locomotor stimulant, either external or internal. Since insects usually take off into the wind and continue to fly in that direction, it might be expected that, through evolutionary processes, food odors functioning as locomotor stimulants would also come to function as orientation stimuli, that is, as attractants. This often seems to be so. In other circumstances, a flying insect has the best chance of picking up an airborne odor stimulus if it flies across the wind, and there is some evidence that this occurs. Most olfactory receptors of insects are on the antennae, so that the insect equivalent of the vertebrate sniff is the waving of its antennae to increase the volume of air sampled. Flight has the same effect. The odor stimuli are rarely those of the actual nutritive components of the food but are tokens representative of the food: floral scents for insects seeking nectar; essential oils for phytophagous species; decomposition products for scavengers; and carbon dioxide, water, and other unidentified skin emanations for bloodsucking insects.

Contact with the food often results in a so-called contact chemical stimulus or taste that terminates the search of the insect and initiates feeding, although this behavior may also be caused by an olfactory stimulus. Taste receptors are present on the tarsi and mouthparts. Those on the tarsi are in association with touch receptors, which inhibit locomotion; they may also induce movements of the mouthparts; e.g., the black blow fly *Phormia regina* Meigen, lowers the proboscis when the tarsal receptors contact sugar solution. The receptors on the mouthparts trigger the feeding response. In the biting insects, the emphasis is on the movements of the mouthparts themselves, which remove and manipulate fragments of solid food. In the sucking insects, emphasis is on the muscles of the cibarium, pharynx, and foregut wall. These muscles reduce the pressure inside the lumen of the gut, causing reflexes in a connecting tubular passage that are carried to the mouthparts and into the fluid food. The distinction is not absolute, however, in either case. Simultaneous with these responses is the glandular response leading to the release of the salivary secretion and, in the sucking insects, usually the pumping of this secretion into the food by the hypopharynx. In both types of feeding, the continuation of feeding is apparently dependent on the appropriate stimulation of groups of little-studied receptors inside the cibarium and pharynx.

MATING

The behavioral problems associated with finding and identifying a mate are not very different from those of food-finding, especially if inbreeding is to be avoided. (To avoid inbreeding, the insects must not mate with others produced in the same breeding place, but must scatter over a large area before they begin the search for mates.) Many different stimuli and responses may be involved, sometimes linked together in a rather rigid way as a chain of reflex responses in courtship behavior. Also, there is very often a rather specific olfactory orienting stimulus of a token nature, the sex attractant, usually produced by the female. Specific differences in attractant odors may play a major role in maintenance of reproductive isolation, such as between several species of *Drosophila*. Such an odor or a different material produced by either sex, may provide an essential stimulus of an aphrodisiac nature before copulation takes place. This may also be of a token nature, but in the sperm webs of spiders the seminal fluid itself seems to be operative. The production of the chemical stimuli is usually terminated abruptly after mating.

When a fertile male has made contact with a virgin female of the same species, the proper positioning of the two sexes is necessary before copulation can take place. This accomplishment may be partly associated with a stimulus that might be called a microattractant, although it has some of the properties of an arrestant. In the grayling butterfly, *Cercionis pegala* Fabricius, for example, as courtship proceeds, the antennae of the female and the scent scales on the forewings of the male must be brought into contact before the female becomes receptive. In some cockroaches, the mouthparts of the female must have access to the tergal gland on the abdomen of the male.

OVIPOSITION

A female insect searching for an oviposition site is very often essentially seeking a source of food for her forthcoming young. To this extent her behavior resembles that associated with feeding. The females of insects that use the same food as their larvae may lay their eggs in their own food material. Adult dung beetles (*Scarabaeidae*), for example, are attracted by the ammonia and skatol of dung, whether they be males or virgin females seeking food, or gravid females seeking oviposition sites. *Drosophila* spp. feed on and lay eggs in fermenting fruit.

In the parasitoid Hymenoptera, most Lepidoptera, and many plant-feeding bugs, beetles, and flies, eggs are usually deposited in or on the host or the food plants; therefore, the entire behavior pattern may be a very close replica of a feeding pattern. The principal difference arises after contact has been made, when identification is commonly the function of receptors on the tarsi, cerci, and genitalia rather than on the tarsi, antennae, and mouthparts. The stimuli are only partly chemical and comprise both arrestants, keeping the female at the site, and ovipositional stimulants, which initiate the preparation of the site and the deposition of eggs. In many agromyzid flies the parallel is even closer, since the food plant of the larvae is identified by the female adult tasting, with the mouthparts, the sap from a trial oviposition puncture.

Often, however, the eggs must be laid where food will become available at the appropriate season, which may be from days to many months ahead. Parasitic tachinid flies lay their eggs on the food plants of their hosts; for them, components of the plants must serve as token stimuli totally different from the food requirements of their offspring. For many insects that are aquatic in their immature stages, water in the vapor phase may be an important attractant stimulus to a gravid female. The oviposition site, when reached, may be identified by the stimulus of the water itself and perhaps by additional stimuli created by dissolved salts and decomposition products of associated organic materials. These additional materials may be indications that by the time the eggs hatch the water will contain appropriate larval food material.

OTHER ACTIVITIES

There is some evidence that chemical stimuli that may be appropriately referred to as species attractants play a part in the assembly of some insect species into crowds or swarms. Some controversy exists about the significance of swarms, perhaps partly because the significance differs between species. Sometimes the stimuli are a step in the process of bringing the sexes together (see discussion on mating); sometimes they seem to be associated with migration and dispersal; and often they are a prelude to hibernation when mutual metabolism provides the group with a termperature advantage. Some species are able to develop normally and maintain themselves only if the population density is held above a critical level by aggregation.

A combination of two or three compounds secreted by the males of an engraver beetle, *Ips confusus* (LeConte), and excreted with the frass attracts females and other males. A mass attack sufficient to kill a tree is essential to survival of the species, since the beetles cannot reproduce in a live tree.

Some aggregations of insects, notably those of a family nature, have an evolutionary relationship to the development of social life. Where this relationship is highly developed, as in the termites, bees, wasps, and ants, chemical attractants, indicator substances, and pheromones play a dominant role in the life of the community. These materials are significant in route-finding, regardless of its objective; in recognition; in communication; and in the maintenance of a balance between the populations of the various castes.

Activities in relation to attractants have sometimes been diverted from their orginal significance to an insect. Flowers of *Arum maculatum* Linnaeus and of the African fly flower, *Stapelia* spp., have the odor of putrid meat and are pollinated by flesh flies, which presumably visit them with the intention of ovipositing. Orchid species belonging to the genus *Ophrys* are each pollinated only by a particular species of sphecid wasp, which attempts to copulate with the flower. The flower resembles the female wasp in appearance and secretes an attractant odor closely similar to that of the female insect.

METHODS

RECOGNITION

Some of the earliest observations on insect behavior were concerned with the attraction of insects to certain foods, extracts of plants, animals, and chemicals. Little chemical knowledge can be gained from references to attraction of foods such as sliced cucumbers, crushed bananas, and fish meal, because of their complex composition, but certain observations of attraction to chemicals fall into a pattern. For example, ammonia, amines, sulfides, and fatty acids have been reported to attract many species. These compounds are products of decomposing organic matter and apparently represent a source of food to the insect. Many insects, especially in the order Diptera, instinctively oviposit in the vicinity of these chemicals, thus providing food for their young. The identification of the specific compounds in natural food mixtures functioning as attractants, arrestants, or feeding or oviposition stimulants permits the synthesis of stable lures that are sometimes more effective than the mixtures. The full extent to which sex attractants occur in the insect world is unknown. The more obvious examples of insects attracting mates, as the gypsy moth does, were discovered when males responded to caged or immobilized females. Although such observations are rather few, the interesting possibility remains that sex lures may be prevalent among insect species. Uncertainty arises from our lack of knowledge of insect mating habits. In the case of the European corn borer, *Ostrinia nubilalis*

(Hübner), the existence of behavior characteristic of a response to a sex attractant was not disclosed until the insects were observed under infrared radiation. The honey bee, *Apis mellifera* Linnaeus, has a sex attractant that may be extracted with diethyl ether from the mandibular glands of queens. However, early experiments failed to demonstrate its attractiveness, because the drones (males) did not respond to the extract until materials impregnated with it were suspended from a pole at least 15 ft above ground level.

EXTRACTION

Many methods have been used to extract, collect, and concentrate the chemical agents influencing insect behavior. The sex attractants of the silkworm moth, *Bombyx mori* (Linnaeus), and the gypsy moth are formed in the lateral glands of the virgin female abdomen. The female, able to protrude and retract these glands, regulates the release of the attractant in this manner. Extraction of the abdominal tips with an organic solvent such as petroleum ether, benzene, or alcohol gives a material highly attractive to the male. The glands that produce the sex attractant of the American cockroach have not been located, but extraction of filter papers exposed to the females does give an active solution, as does column chromatography, of an inactive acetone extract. The largest amounts of cockroach sex attractant were obtained by drawing a stream of air through large cans containing thousands of virgin female cockroaches and freezing the volatiles in a dry-ice trap. The lure was recovered from the condensate with an organic solvent and purified by adsorptive chromatography and steam distillation. The amount produced by the females was fantastically small, only 12.2 mg of pure attractant being obtained from approximately 10,000 female American cockroaches by continuous collection over a 9-month period.

Chemical fractionation of the lipids from the honey bee gland yields "queen substance" (*trans*-9-oxo-2-decenoic acid), which is attractive to drones at 0.1 mg per assay tube, and at least two other substances with some attractiveness. Since sex lures are usually much more potent, the queen substance may not be the true honey bee sex lure. Indeed, extirpation of the mandibular glands does not necessarily render a virgin queen incapable of mating, and reconstitution of the lipid complex results in considerably more attractiveness than is shown by individual fractions.

The virgin female of the introduced pine sawfly, *Diprion similis* (Hartig), is capable of attracting exceptionally large numbers of males. One such caged female placed in a field attracted well over 11,000 males. Column chromatography of extracts of females yielded a substance that, though impure, in amounts as small as 0.004 mg attracted 500 to 1,000 males within 5 minutes.

Activities of an attractant in some types of extracts is often masked, but a potent extract may be recovered by chromatography.

CHEMICAL IDENTIFICATION AND SYNTHESIS

The chemist faces a formidable task in his attempt to isolate the active principle of a natural product. He has to devise an extraction procedure and have a means of assaying the biological activity of his preparations. The active principle may be unstable. It may be present in minute amount, only in certain parts of the source, or only at certain times. High volatility may also be a consideration. If he isolates the lure, he has to identify it. Usually the more potent the chemical, the less will be found in the crude extract. Too often the amount available is exceedingly small.

A chemist limited to the classical procedures available 15 or 20 years ago would have great difficulty determining the chemical structure of a few milligrams of a complex unknown compound. Fortunately, electronic instrumentation has revolutionized chemical apparatus. Today, gas chromatography, infrared, ultraviolet, nuclear magnetic resonance, and mass spectrometry are available. These techniques are essentially nondestructive and require only small samples. Thus, deciphering chemical structures at the milligram level is now possible, and this improved methodology is helping chemists solve problems that for years have resisted solution.

Most of the potent lures in current use are not natural products but were found by the synthetic approach. Pure chemicals are exposed to a given insect species to determine which of them influence behavior. Compounds related to the best candidates are then tested to achieve greater activity. At first, screening may be random, but chances of turning up leads are greatly improved if large numbers of chemicals of many different types are tested. Shelf or available chemicals are not sufficient. Synthesis is necessary to furnish unavailable candidates. For efficient screening, it is most desirable that testing be reliable and rapid, that only a small sample be required, and that a ready supply of insects be available, preferably throughout the year. Examples of some synthetic attractants found by this approach are listed in Table 4, along with the natural bombykol from the silkworm and the natural gypsy moth lure, both of which have been made synthetically.

ASSAY

The screening of candidate insect attractants and associated agents is not as straightforward as the screening of insecticides. A suitable bioassay must be built around the natural habits and idiosyncrasies of each species of insect.

TABLE 4 Potent Attractants Made Synthetically

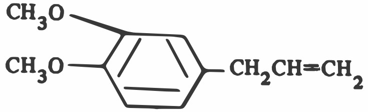
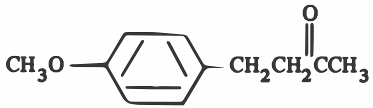
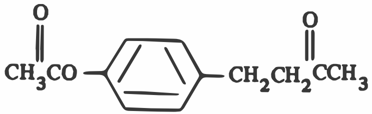
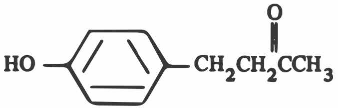
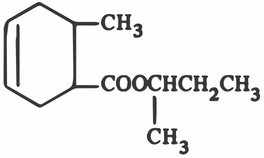
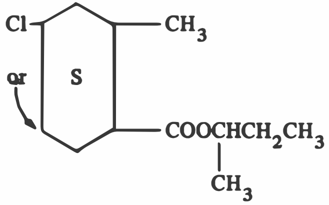
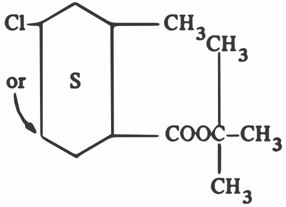
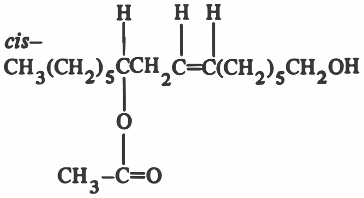
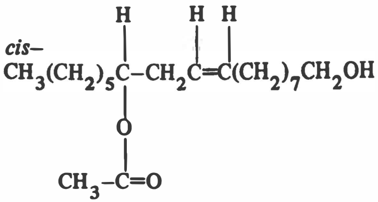
Common Name	Structure	Species Attracted	Other Species Attracted
Methyleugenol[a]		Oriental fruit fly, *Dacus dorsalis* Hendel	*Dacus umbrosus* Fabricius
Anisylacetone		Melon fly, *D. cucurbitae* Coquillett	Queensland fruit fly, *D. tyroni* (Srogatt) and *D. ochrosiae* Malloch
Cue-Lure[a]		Melon fly	Queensland fruit fly
–		Melon fly	
Siglure		Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann)	Walnut husk fly, *Rhagoletis completa* Cresson

TABLE 4 Potent Attractants Made Synthetically (Continued)

Common Name	Structure	Species Attracted	Other Species Attracted
Medlure		Mediterranean fruit fly	
Trimedlure[a]		Mediterranean fruit fly	Natal fruit fly, *Pterandrus rosa* (Karsh)
Natural lure of gypsy moth[a]	 $\text{cis-}\ CH_3(CH_2)_5\underset{\underset{CH_3-C=O}{O}}{\overset{H}{C}}CH_2\overset{H}{C}=\overset{H}{C}(CH_2)_5CH_2OH$	Gypsy moth, *Porthetria dispar* (Linnaeus)	–

Gyplure	 $cis\text{-}CH_3(CH_2)_5\overset{H}{\underset{\underset{CH_3-C=O}{O}}{C}}-CH_2\overset{H}{C}=\overset{H}{C}(CH_2)_7CH_2OH$	**Gypsy moth**	–
Bombykol[a]	*trans*–10, *cis*–12– $CH_3CH_2CH_2CH=CH-CH=CH-(CH_2)_8CH_2OH$	**Silkworm moth,** ***Bombyx mori* (Linnaeus)**	–
Butyl sorbate[a]	$CH_3-CH=CH-CH=CH-COOC_4H_9$	**European chafer** ***Amphimallon majalis*** **(Razoumowsky)**	–
Methyl linolenate[a]	$CH_3-CH_2-CH=CH-CH_2-CH=CH-$ $CH_2-CH=CH-(CH_2)_7-COOCH_3$	**Bark beetles,** ***Ips typographus*** **(Linnaeus) and** ***Hylurgops glabratus*** **(Zetterstedt)**	–

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[a] **Most effective lure for insect under Species Attracted column.**

Few gypsy moths, for example, seek a mate on a cloudy day, and even very attractive preparations are ineffective on such days. The southern armyworm, *Prodenia eridania* (Cramer), which responds to its sex attractant in the early morning hours (between 3 and 5 AM) is indifferent to the same stimulus at other times. A satisfactory olfactometer for fruit flies is an 8-ft-cubical screened enclosure containing about a dozen traps suspended from a slowly rotating wheel, since in their natural environment the flies respond to the lures while in free flight. Crawling insects have been offered a choice of two air streams of identical composition except that one contains a chemical vapor.

Testing is further complicated by the effect of vapor concentration on attraction. Too low a concentration of vapor will not be detected, and too high a concentration may repel. Several dilutions of the chemical should be tested to avoid missing a good attractant. For trapping purposes, the ideal lure should attract at concentrations ranging from high to low, a property that implies effectiveness at both small and great distances from a baited trap.

Laboratory tests have certain advantages: conditions such as light, temperature, and humidity, may be standardized and made constant or varied; insects may be raised under controlled conditions; and tests may be conducted throughout the year. An important requirement for laboratory testing is that a method for rearing large numbers of insects should be available. Efforts to rear certain insects in the laboratory have been unrewarding because of the high incidence of disease that is fatal to the larvae. This has handicapped progress in the search for behavioral control agents for some species. Even with good test insects, difficulties may be encountered because of daily or seasonal variations in insect activity, and some insects do not respond to a lure until they reach a certain physiological state.

Laboratory tests alone have certain drawbacks; e.g., it is possible that in rearing insects in the laboratory through many generations, the responses of the insects to certain lures may change from those of their wild counterparts. The method of exposing the chemical is important. The chemical may be offered to the insect on paper, in solution or emulsion, or on a wick. The insects on an arrestant may be counted after a definite time interval, or counts may be made of those drawn by an attractant into a trap that contains a toxicant, adhesive, or other retaining means.

The ultimate test of a behavioral control agent must be made in the field, where the lure competes with the many stimuli the insect meets in its natural habitat. Unfortunately, laboratory and field evaluations often do not agree. A study to determine basic reasons for such differences might lead to the development of laboratory test methods that would give closer correlation with results obtained in the field.

For insects that cannot be reared in the laboratory, the use of field tests, although entailing considerable labor, is a valid initial recourse. Such tests can only be made during a limited season and are subject to variables such as light, temperature, humidity, weather conditions, insect density, age of population, and competing natural stimuli. As in laboratory tests, the use of a standard chemical, if one is available, is of considerable help in minimizing the many variables.

UTILIZATION IN CONTROL

DETECTION AND SURVEY

Lures offer a remarkably simple means of detecting insects (see Chapter 3). A trap is baited with a lure and the responding insect is caught, signaling the presence of the species. A lure specific for one species eliminates the necessity of having trained personnel sort out the desired insects from a miscellaneous collection caught by unselective methods. Several of the insect lures in traps are now standing guard at various borders, mainly at ports of entry. The traps assure the early detection of an infestation, which may then be eradicated before it can enlarge; the traps do the job at a very small cost. When an infestation becomes established—as happened with the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), in Florida in 1956, 1962, and 1963—the value of this technique becomes even greater, because traps can pinpoint the exact location of the insects. Attractants thus increase the efficiency of insecticide applications, because treatments need be applied only where insects are caught and only as long as they are caught. Money is saved because insecticides are not wasted, and residue problems are held to a minimum. Liquid lures of corn or cottonseed protein hydrolysate are used routinely in traps along the United States border with Mexico to detect invasion by the Mexican fruit fly, *Anastrepha ludens* (Loew). Traps baited with attractants are also used in annual surveys to determine the extent of infestations of the gypsy moth and the Japanese beetle, *Popillia japonica* Newman.

Although many highly attractive chemicals have been extracted from natural sources, or produced in synthesis programs, such isolation and synthesis are not always necessary for effective employment in survey work. Crude extracts—clipped abdomens of insects and live insects—have been used with success. Many attractive materials that are ineffective as control agents may be utilized effectively in survey work.

CONTROL

Attractants and associated agents may be used in several ways for controlling insects, as well as for gathering fundamental information about pests, which might lead to their control. Insects may be lured into traps by the chemical and then killed. A toxic material or a culture of pathogens may be mixed with an attractant or feeding stimulant to destroy the males. A chemical may also be used to attract large numbers of insects that can be sterilized and released among the native population to reduce pest numbers.

Traps

The number of insects caught in the field depends not only on the potency of the attractant, but also on the design of traps and their placement (see Chapter 11). Color, size, and shape are important in trap design. The latest gypsy moth trap, made of cardboard with a plastic one-way entrance at each end, depends on an adhesive to ensnare moths responding to the sex lure placed inside the trap. Air-dropped into infested areas, these traps are designed to attract male gypsy moths, which will be kept from mating. Another type of trap is extensively used for detecting fruit fly infestations. A chemically baited wick attracts the insects inside the trap, where they are overcome by a fast-acting volatile insecticide, such as dichlorvos, lindane, or naled. A trap used for the European chafer, *Amphimallon majalis* (Razoumowsky), has twin baffles set above a collecting cone; the heavy beetle strikes the baffle and falls into the poison jar.

Air movement is important in trap placement. Traps situated upwind from an infestation are more likely to catch insects than those down or across wind. Traps in hollows or surrounded by dense growth do not catch well because of restricted air movement. Odors of chemicals tend to sink to the ground, because they are almost always much heavier than air. The behavior of the male gypsy moth is apparently adapted to this property of odors, since this insect flies long distances close to the ground. Catches of this moth in traps placed between ground level and 6 ft above showed little difference but fell off at the 12-ft level. A mosquito, *Culex pipiens quinquefasciatus* Say, responds to oviposition attractants only at similar low levels above the ground.

The advantage of combining sex attractants with light traps to increase catches has been established for several species, including the tobacco hornworm, *Manduca sexta* (Johannson), and the cabbage looper, *Trichoplusia ni* (Hübner), but much more research is needed to determine the potential of the combination of biological and physical attractants in the management of total insect populations over large areas.

With Insecticides

The use of an attractant or feeding stimulant in combination with an insecticide sometimes provides a high degree of insect control without the necessity of complete spray coverage. Even attractants that affect only the male can provide good control if they are sufficiently powerful. The oriental fruit fly, *Dacus dorsalis* Hendel, was eradicated from the Pacific island of Rota by aerial distribution of 5- × 5-cm fiberboard squares saturated with a bait containing an insecticide, naled, and an attractant, methyleugenol. This lure is highly attractive to male oriental fruit flies, which also feed on it ravenously, but is generally unattractive to the females. Control of males was so complete that the female flies were unable to reproduce, and 15 biweekly treatments resulted in the eradication of the species from the 32-square-mile island. Only 3.5 g of insecticide per acre were needed with this highly specific lure. Interesting observations having practical significance regarding the attraction of female oriental fruit flies to methyleugenol have been reported. When the male population is greatly reduced, substantial numbers of females are attracted to the chemical lure. Presumably, females become responsive to the chemicals when mating opportunities are not presented.

With Pathogens

It seems probable that the efficiency of some insect pathogens could be increased by using attractants and feeding stimulants to obtain maximum contact between the pathogens and their hosts. In laboratory experiments, the incidence of infections of larvae of the corn earworm, *Heliothis zea* (Boddie), with nuclear polyhedrosis virus, and infections of boll weevils with a sporozoan, *Mattesia grandis* McLaughlin, were significantly increased when feeding stimulants were applied with the infective material to the leaves or plants on which the insects were exposed. The efficiency of pathogens in combination with attractants has not been demonstrated in field studies, but it offers a promising area for research.

With Sterilants

The maximum utilization of insect chemosterilants depends greatly on the development of efficient attractants and related agents. Chemosterilants can be more effective than toxicants in reducing natural populations of insects, since the treated insects are not removed from the population but remain to compete with untreated males and females for mates. They can be used most effectively and safely in connection with attractive chemicals or radiations that will draw a large proportion of a pest species, and only the pest species, from a wide area to a place where the insects and the chemosterilant can be brought together without hazard to other organisms. Arrestants and feeding or mating stimulants will assure adequate contact between the pests and the bait or treated surface. Sugar baits containing various chemosterilants have given control of house flies in poultry houses, and combinations of chemosterilants with fruit fly lures have reduced infestations of mangoes with the Mexican fruit fly in small field tests. Much research is under way in this area which should provide numerous demonstrations of the value of attractants and associated agents in connection with chemosterilant techniques. The sterilization of natural populations of insect pests is inherently the most effective population-suppression method, provided both sexes are sterilized. The sterilization of one sex only, such as males coming to sex lures, may have no material advantage over killing the same number of males in a continuing trapping program. The sterilization of females only when attracted to sex lures or to feeding or oviposition stimulants could have a greater effect on suppression of the population than the destruction of a like proportion of the females.

ALTERATION OF NORMAL BEHAVIOR

Many insects, particularly the monophagous and oligophagous species, are guided to their host plants and stimulated to feed, oviposit, and even disperse, by a chain of stimuli resulting from chemical and physical forces originating from the host plant. An understanding of the basic mechanisms involved in host selection by an insect for food and oviposition provides an opportunity to manipulate these factors to trick or confuse the insect to self destruction. Some possibilities envisioned or under investigation in this area are:

1. Treatment of weeds and other undesirable plants with insect attractants, feeding stimulants, and oviposition stimulants to create susceptibility to an insect. Materials need to be highly active in order that the treated plants compete with normal host plants in nature.
2. Treatment of host plants to induce greater susceptibility for purposes of luring insects to specifically treated portions of a crop. This method presents greater possibilities than treatment of weeds, because a preference which already exists may be increased with less effort than that needed to create a preferred host from a nonpreferred plant
3. Use of chemicals to distort sexual activity, diverting the males or females in their search for mates, or confusing their orientation mechanisms.

BENEFIT FROM RESEARCH

To obtain the maximum benefit from research on insect attractants and related agents, we must be prepared to adopt programs for controlling insect populations over large areas. Attractants provide no protective shield against insect attack or invasion as do residual insecticides. Adequate protection will be achieved only by reducing the population level within the flight range of the species to a point at which the number of insects remaining will not constitute a hazard. Many species are highly mobile, and attractants can be practical only if they are highly effective and are used against the total population in an area large enough to keep infiltrating forms to levels of no economic significance.

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CHAPTER 14

Chemical Repellents

In the course of his development, man learned that certain materials, usually of plant or animal origin, discouraged attack by insects and related pests. Such materials have included smoke from wood fires, burning hemp, punk, and even camel's urine. About 80 years ago, several essential oils, including oil of citronella, were advanced as mosquito repellents. These repellents (for use on humans) have been replaced by highly effective synthetic materials that evolved from the screening of organic chemicals produced in the laboratory. It is now known that chemicals need not be malodorous to humans in order to repel certain arthropods. Less use has been made of repellents for the protection of animals and plants than for the protection of man, but additional research should greatly expand the usefulness of this method for the control of all types of arthropod pests.

Systematic search for repellents among the synthetic organic chemicals began in the late 1930's, when techniques were developed for obtaining reproducible quantitative measurements of the protection time afforded by repellents when applied to human arms exposed to caged mosquitoes. Several effective mosquito repellents, e.g., ethyl hexanediol, dimethyl phthalate, and butyl 3,4-dihydro-2,2-dimethyl-4-oxo-2H-pyran-6-carboxylate, were available at the outbreak of World War II. However, the requirement for maximum protection of military personnel against a wide variety of disease vectors stimulated a manifold increase in the synthesis and evaluation programs. More than 15,000 compounds have now been tested as repellents. Although many of these compounds were effective against insects, few could be used. Compounds to be placed on human skin or clothing must be nontoxic, nonirritating, nonallergenic, harmless to wearing apparel, inoffensive in odor, long-lasting, and stable to sunlight. They should also be effective against as broad a spectrum of insects as possible. Repellents should withstand conditions that induce sweating by the host, resist loss by wiping, and if used on clothing, resist leaching by rain and laundering. These requirements are so restrictive that only about 20 of the compounds are safe enough for use on human skin. The repellent that best meets all these requirements is deet (*N,N*-diethyl-*m*-toluamide).

Concurrent with these developments, attempts to find repellents useful for protecting livestock and agricultural products from insect attack have gone forward, but on a much smaller scale.

CHEMICAL REPELLENTS

A repellent, in the strictest sense, is a chemical that causes an insect to make oriented movements away from its source. The distance the insect need move, however, is usually much shorter than the distance it does move in response to an attractant; ordinarily, it need only leave or avoid a treated surface, or at most move a few centimeters out of the effective concentration of repellent vapor. Because of the short distances of travel involved, it is sometimes difficult to differentiate between a true repellent and a general irritant, if indeed there is a difference.

Most repellents are volatile and are active in the vapor phase. When enough repellent is on a surface, an effective concentration of vapor prevents insects from alighting. A lower quantity of repellent on the surface may allow insects to alight momentarily before they are repelled.

Repellents are, however, quite distinct from feeding or oviposition deterrents. Deterrents do not prevent the aggregation of insects on a given surface or in a given area, as repellents do, but they inhibit the feeding or oviposition by insects when they are present in places where the insects would, in their absence, feed or oviposit. Feeding deterrents are discussed in Chapter 12.

The same chemical may function at several levels of effectiveness. For example, when a mosquito repellent such as diethyltoluamide is applied to the skin it provides a period of protection during which mosquitoes are prevented from alighting. However, the repellent is gradually lost from the skin by evaporation, absorption, and abrasion, and eventually a dosage level is reached at which the mosquitoes are able to alight but are immediately driven off. At this level the repellent action is virtually indistinguishable from that of a general irritant. As the dosage becomes still further depleted, the mosquitoes may remain on the skin but not bite. Often they walk about, touch the skin with the palpi, and then rub the palpi with the tarsi as though to clean them. At this dosage level the diethyltoluamide is acting as a feeding deterrent, not as a repellent. Finally, the dosage is depleted to a level that will not prevent biting.

With most repellents the margin between the minimum dosage that prevents alighting and the maximum dosage that permits biting is quite small; therefore, at high temperatures the repellent dosages remaining on the skin pass through the second and third stages very quickly, but, at low temperatures, which reduce the rate at which the repellents are evaporated, these stages are more prolonged.

Chemicals with extremely rapid knockdown action, although not repellents in the strict sense, are discussed with repellents in this chapter, since the end results in the protection of the host from insect attack are similar. For the same reason, this chapter will also include a discussion of the knockdown agents used for personal protection from chiggers (larvae of mites of the genus *Trombicula*).

SOURCES AND DEVELOPMENT

SOURCES

Basically, there are two chemical approaches in searching for insect repellents: the empirical approach, which involves the testing of a wide variety of compounds to develop leads; and the isolation–identification approach, which is aimed at recognizing a naturally occurring repellent, isolating it in pure form, determining its structure, and ultimately synthesizing it or a biologically active analog.

The synthesis program starts with completely random screening. As structural leads are uncovered and related compounds are synthesized, a much higher percentage of biologically active compounds invariably results than is obtained by screening a random assortment of chemicals.

DEVELOPMENT

Problems related to methods of finding repellents are similar to those of finding attractants; however, bioassay techniques vary. Of the two approaches, empirical and isolation–identification, employed while searching for a repellent, the empirical approach has proved most successful. Two products, barthrin and dimethrin, which are related to the pyrethrins and possess repellent properties, are the results of both isolation and screening techniques.

Progress in finding repellents by the empirical approach depends on the rapidity and reliability of screening procedures. Although the ultimate test must be made in the field, the development of laboratory tests under controlled conditions has greatly accelerated progress. In these tests a chemical is interposed in some fashion between insect and host, and a measure of deterrence is derived, e.g., duration of effective action or number of bites in a given time, or both.

No one bioassay will be useful for all arthropods, since each species has its own specific preferences. In setting up the bioassay, consideration must be given to means of rearing insects, age or life stage of insect to be tested, avidity of insect (should be checked just before test if possible), means of measuring response (number feeding, speed of knockdown, mortality, number of bites, landing rates, and number staying), environmental factors (temperature, humidity, light, time of day or season, test cage, and air contamination), attractiveness of host, part and amount of host exposed, use of animals in place of humans as hosts, mode of application of chemical, carrier or formulation and amount of chemical, toxicity of chemical to host, means of measuring persistence (exposure to air, sweating, wiping, rain, and laundering between tests), distance of effectiveness, and completeness of coverage of the host. Attempts have been made to regulate these variables as much as possible, but normal biological variation can never be eliminated. To minimize errors, the comparison of candidates with standard materials is a big help. These standards may be run at the same time or interposed regularly or randomly. The number of tests required for significant results is determined by statistical evaluation of data.

The properties of the repellent, both physical and chemical, are important. Volatility relates inversely to persistence. Lipoidal and water solubility relates to absorbability. Corrosive chemicals will harm the host. Chemical functional groups of certain types are associated with repellency. For example, the diethylamides, 1,3-diols, amide esters, hydroxy esters, and diesters possess good repellent activity compared with other types of compounds.

The effective chemicals must still run the gauntlet of pharmacological scrutiny, which may involve studies on absorption; retention; metabolic changes; mode of excretion; damage to delicate tissue, such as might be involved in use on infants; inhalation versus absorption toxicity; residues in end product; and long-time (chronic) effects on various organs.

USES OF REPELLENTS

PROTECTION OF DOMESTIC ANIMALS

The use of repellents for domestic animals is generally limited to the protection of cattle and horses from biting flies: the horn fly, *Haematobia irritans* (Linnaeus); the stable fly, *Stomoxys calcitrans* (Linnaeus); horse flies and deer flies (Tabanidae); and mosquitoes (Culicidae). Studies with repellents have also included the face fly, *Musca autumnalis* De Geer, a livestock pest introduced into the United States about 1952.

Although modern insecticides applied to cattle will provide adequate protection from the horn fly, they will not completely free animals of attack from the horse fly and stable fly. A long-lasting repellent for application to animals to protect them from biting flies would reduce the annoyance and blood loss that result in decreased milk production and lowered weight gain, and would aid in the prevention of disease transmission by flies such as the Tabanidae.

Because numerous variables are involved, e.g., the chemical and its formulation, the physiology of the insect pest, environmental conditions during testing, and the differences in relative attractancy of test animals, it is difficult to interpret results from the many studies conducted on the effectiveness of various repellent chemicals for the protection of livestock against insect attack. Attempts have been made to standardize laboratory screening methods, but the results have been difficult to correlate with those obtained under field conditions. For example, many repellents applied to inanimate objects in the laboratory remain effective for several days to weeks, but when applied directly to an animal, the same materials repel flies for only a few hours at best. Field tests should therefore be incorporated into the evaluation program at an early stage.

Although hundreds of chemicals have been screened as livestock insect repellents, only a few are recommended, and these have only a limited value, primarily because of their short residual effectiveness. A repellent considered excellent for man might be of little value for livestock because of the high dosages necessary and the need for frequent application. Conversely, the most widely recommended and effective materials for the protection of cattle are synergized pyrethrins, which are unsatisfactory as repellents for man because they permit the insects to land and bite briefly, even though they quickly withdraw. Synergized pyrethrins have an obvious irritating effect on the insect and exhibit an unusually rapid knockdown of insects contacting them, which probably accounts for much of their apparent tactile repellent property. Even with compounds of this type, however, the residual effectiveness is of short duration, usually only 1 to 2 days. Materials such as butoxy polypropylene glycol; dipropyl pyridine-2,5-dicarboxylate; 1,5a,6,9,9a,9b-hexahydro-4a (4*H*)-dibenzofurancarbox-aldehyde; 3-chloropropyl octyl sulfoxide; and dibutyl succinate have also received limited use as components in livestock spray formulations. These chemicals are usually incorporated into formulations containing either pyrethrins or a nonrepellent insecticide, and it is therefore difficult to determine their actual value in protecting cattle from insect attack. In most cases in which these materials have been applied alone to cattle, the protection time has been no more than a few hours, seldom exceeding 24 hours. When repellent chemicals have been combined with pyrethrins, the primary protective action has probably been brought about by the pyrethrins. However, the use of an additional repellent has sometimes made it possible to reduce the amount of pyrethrins without decreasing the effectiveness of the repellent treatment.

Chemical repellents may be applied to livestock by covering the entire body of animals with wet sprays (1 to 2 qt per animal), low-volume mist sprays (1 to 2 oz per animal), or dust formulations. For protection from the face fly, sprays directed only to the head and neck have given results comparable to whole-body sprays. To protect dairy cattle from the face fly, repellents may be painted or wiped onto the faces of animals held in stanchions. Application of repellents with barn-fogging devices and back rubbers has not been very successful. Regardless of the method of application, currently known repellents have a short residual effectiveness and must therefore be applied to animals frequently. For this reason, automatic sprayers that allow for the self-application of repellents by the animals may be of potential value. There are indications that practical protection from all biting flies is possible if animals are subjected to pyrethrins or pyrethrins-repellent sprays applied at least twice each day with an automatic sprayer.

Repellent chemicals commonly used in livestock sprays are relatively nontoxic to mammals and may be used at fairly high concentrations and at frequent intervals. This applies even to dairy cows, with which the problem of pesticide residues is especially critical because of possible contamination of the milk. In various screening programs, however, a number of promising repellent chemicals have had to be discarded because of their toxicity to animals treated with amounts sufficient to provide protection from insects.

Although no longer used extensively, pine tars and phenolic compounds served in the past as wound-dressings to protect animals from attack by screwworms and blow flies. Materials that provided protection may have achieved repellency by masking the attraction of the wounds, by toxic action, by true repellency, or by a combination of all three actions.

Considerable research has been directed at developing materials that exhibit systemic repellent action. The materials could theoretically be administered either orally or by injection to render animals repellent to biting insects. The results of these efforts have been negative, but the area deserves more attention.

PROTECTION OF MAN

Effectiveness of Repellents

Repellents play a small but important role in the protection of man from attack by annoying and disease-bearing insects. The best way to obtain protection from biting insects is, of course, to destroy the insects, and the use of repellents cannot substitute for a satisfactory control program, when such a program can be adequately and economically conducted. In many situations, however, control programs are impossible or impractical, especially when the infested area is large and undeveloped, the number of persons exposed is small, or the period of exposure is temporary. Repellents are generally less satisfactory than immunization, or even chemical prophylaxis, in providing protection from insect-borne diseases, but such methods of prevention do not exist for some diseases. In such situations it becomes necessary for the individual to rely on methods of personal protection. When properly applied, repellents are completely effective against chiggers, and clothing treatments have repeatedly provided complete protection against scrub typhus for large troop units deployed in infested areas. Repellents are highly but not completely satisfactory for use against ixodid ticks, fleas, mosquitoes, stable flies, and some other species of biting Diptera. If they are applied regularly and properly, they can greatly reduce the risk of infection with the diseases carried by these pests. Repellents have been ineffective against some other Diptera, such as tabanids and tsetse flies (*Glossina* spp.), and no repellents for argasid ticks have been reported.

None of the known insect repellents for the protection of man are ideal. They have some odor, they feel oily, and they soften paint and some plastics. They must be applied at rather massive dosages, in the range of 2 to 4 mg/cm^2 of skin. They are effective for only a few hours, since they are lost from the skin by evaporation, absorption, and, most importantly, by being rubbed off on clothing or other objects. However, insect repellents play a significant role in protecting men from arthropod-borne diseases, and they are a much welcomed protective measure for sportsmen and others who encounter hordes of mosquitoes or other pests in their favorite recreational areas. In certain situations, repellents make it possible for people to work or enjoy outdoor recreations when they otherwise could not take part in such activities. Many military operations would be greatly hampered without repellents. Troops cannot perform their duties efficiently when swarms of pests make mere existence almost intolerable.

Research on repellents for the protection of man, including studies of the physiology of the sense organs of insects, still provides a challenging and potentially profitable area of investigation.

Additional research is needed to discover or synthesize repellents that are free from the undesirable features mentioned above, or that will remain effective longer when applied to the skin. Compounds that will have a systemic repellent action when taken orally, i.e., repellent pills, are very desirable. Studies to elucidate the factors that influence biting by mosquitoes may lead to the development of such repellent materials, and the prospect justifies the best combined efforts of entomologists, physiologists, chemists, dermatologists, and specialists in related fields.

Skin Applications

An acceptable degree of relief from annoyance by pest mosquitoes is usually obtained by applying repellents to the exposed surface of the skin (Figure 36),

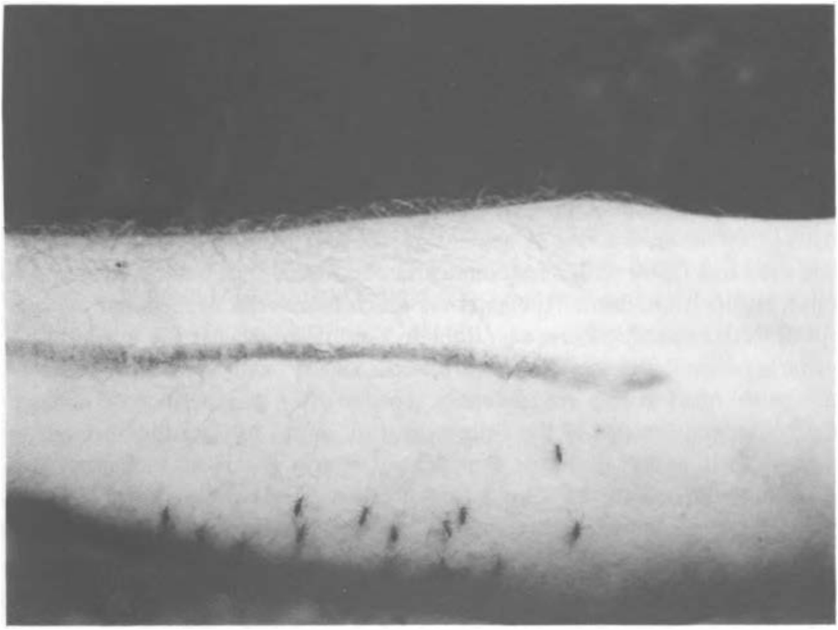

FIGURE 36 **Mosquitoes, *Aedes aegypti* Linnaeus, bite readily on an untreated area of an arm but avoid a portion (above the black line) treated with a repellent. (USDA photograph)**

but for complete protection, especially against disease vectors, it is also necessary to treat the clothing; clothing treatments are essential for protection from fleas, ixodid ticks, and chiggers.

The most economical formulation for application to the skin is the undiluted repellent or a high concentration of the repellent in a cosmetically favorable solvent such as alcohol. The repellent is shaken from the container into the palm of the hand and spread evenly over the exposed skin, with care to avoid getting it into the eyes. Pressurized spray containers are popular and are used in the same way to treat the skin; they are more convenient than bottled repellents for treatment of clothing. Repellents are often incorporated into creams, lotions, and powders, sometimes in combination with other functional ingredients such as suntan oil or emollients. Hundreds of additives, such as salts, oxides, silicones, antioxidants, antiperspirants, greases, and resins, have been tested in an attempt to extend the protection period of repellents, but none has been effective. One possible exception is zinc oxide; formulations containing 40% or more of repellent and 5 to 10% of zinc oxide sometimes protect as long as full-strength repellents, but never longer.

The period of protection given by a repellent varies with the chemical, the individual, the environment, and the species and avidity of the insects. The minimum dosage that provides complete protection at the time of application may vary as much as 30-fold between repellents, e.g., between diethyltoluamide and dimethyl phthalate against the yellow-fever mosquito, *Aedes aegypti* (Linnaeus). Some individuals lose repellents faster than others by evaporation and absorption, and the activity of the individual has a marked effect on the rate at which the repellent is lost by rubbing. Repellents are lost faster under environmental conditions that induce sweating and rapid evaporation. Some repellents are much more effective against certain species than against others, e.g., dimethyl phthalate against the common malaria mosquito, *Anopheles quadrimaculatus* Say, and the yellow-fever mosquito. Most insects are less easily repelled after long periods of fasting; e.g., 8-day-old females of the yellow-fever mosquito bite readily through dosages of dimethyl phthalate that protect against 2-day-old females.

Effective repellents are found among diverse classes of chemical compounds. Materials that have proved outstanding for one or more uses include such compounds as deet; ethyl hexanediol; dimethyl phthalate; dimethyl carbate; and butyl 3,4-dihydro-2,2-dimethyl-4-oxocarboxylate.

Clothing Treatments

Repellents for protection against ixodid ticks and chiggers must be applied to clothing rather than to the skin. Little has been reported on the practical use of flea repellents, but it seems probable that both skin and clothing treatments would be required for both fleas and mosquitoes. The common mosquito repellents act more as knockdown agents than as true repellents against chiggers, and some compounds that are not effective against other species, such as benzyl benzoate, are outstanding against chiggers. Clothing must be treated at a rate of 2 to 3 g/ft^2 (930 cm^2) to provide protection through several days or weeks of wear. The repellent may be applied as a spray or by saturating the clothing with an emulsion of the repellent, or a solution in a volatile solvent, and allowing the clothing to dry before it is worn.

Systemic Repellents

The search for systemic repellents is being pursued with renewed emphasis. The folklore of many races includes belief in herbs or chemicals that, when ingested, prevent insect bites. Belief in the effectiveness of sulfur is particularly widespread and has carried over to modern sulfur-containing compounds such as thiamin hydrochloride. Despite repeated failures to demonstrate any effectiveness in these compounds in controlled experiments, it is hard to shrug off the possibility that under some special conditions they might have conveyed some repellency, and that their potential might be increased and exploited by adequate research. The success with systemic insecticides for the control of animal pests has also added to the interest in systemic repellents. Current research effort is along the following lines: (1) empirical testing of compounds; (2) attempting to synthesize compounds containing both a moiety known to be repellent, e.g., deet, and a moiety known to be deposited in the skin following ingestion, e.g., griseofulvin; (3) finding naturally repellent individuals and determining the reasons for their repellency; and (4) learning more about the natural attractants and repellents in the skin as a basis for devising ways to decrease or counteract the attractants and increase or synergize the repellents, or both.

Special Precautions

Because of their method of use, recommended repellents have a wide margin of safety; about the only precaution necessary is to avoid getting them into the eyes. However, some repellents are recommended for use on clothing only, and these should not be applied directly to the skin. Care should be taken to protect valuable varnished or painted objects, and some plastics, from damage resulting from contact with repellents. The repellents must not be taken internally.

PREVENTION OF INFESTATION IN LIMITED AREAS

Outdoor Areas

Smoke has long been used to drive mosquitoes and other insects from outdoor areas, and it is about as effective as any other agent acting as a repellent in distinction from an insecticide. Burning pyrethrum has some repellent as well as insecticidal action. Other repellents mentioned have little effect when volatilized by burning or atomization, since adequate concentrations cannot readily be maintained in outdoor areas, and shifting air currents disperse the vapors in undesired directions.

Buildings

Termites Although certain woods are resistant to termite attack, it is doubtful that any possess complete immunity to all species of termites. Specific chemicals in the wood apparently contribute most of the resistance. Pinosylvin monomethyl ether from *Pinus sylvestris* L., taxifolin (3,5,7,3′,4′–pentahydroxyflavonone) from Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, and *beta*-methylanthraquinone from East Indian teak, *Tectona grandis* L. f., have protected susceptible woods from attack by a drywood termite, *Incisitermes*

(=*Cryptotermes*) *brevis* (Walker), for periods of 5 to 11 years. Apparently, these compounds act more as feeding deterrents than as insecticides.

Plant extracts, such as beechwood creosote, pine resin extractives, and oil of cedar wood, are used occasionally for the treatment of wood products to impart some degree of resistance to attack by termites and other wood-feeding insects. It is not fully established whether they act as repellents, feeding deterrents, insecticides, or in all three ways, and additional research is needed to elucidate their action.

Various synthetic organic chemicals are employed to deter the destructive action of termites. Some are applied to surfaces of wood or are pressure-impregnated into wood, and others are applied as soil treatments around structures. One example is pentachlorophenol, which is moderately toxic to the eastern subterranean termite, *Reticulitermes flavipes* (Kollar), and also destroys wood-associated microorganisms essential to a termite's diet. At levels above 1,000 ppm in soil, this chemical is repellent to termites through vapor action. DDT, similar in toxicity to pentachlorophenol, elicits a repellent action at concentrations in the soil of 50 ppm or higher. The nature of this repellency is apparently that of contact stimulation and irritant effect and is the early manifestation of a toxic reaction which is still physiologically reversible in the termite. Chlordane, dieldrin, and heptachlor at high concentrations in soil cause an avoidance reaction after brief exposure. This reaction of the insect is associated with toxicity, and, although avoidance of a barrier results, some mortality also occurs. Negative colony response to untoward conditions, supraorganismic in nature, can be expected in a number of situations, and the presence of a barrier that is repelling as a vapor, as a tactile stimulus, or as a toxicant to individuals is an important phenomenon in insect control.

Other Insects Attempts to drive flies and mosquitoes from buildings, or to keep them from entering, by means of repellents have met with negligible success. A few compounds, e.g., dibutyl succinate, discourage roosting by house flies, *Musca domestica* Linnaeus, on treated surfaces, and, if sufficiently heavy applications can be maintained on all interior surfaces, the treated buildings become unfavorable habitats; however, at the necessary rates of application such compounds are expensive and malodorous.

Food and Drink Cases and Small Enclosures

In some circumstances repellents can profitably be used to prevent cockroaches (Blattidae) and other household pests from hiding in beer, milk, or soft drink cases in which they might be transported from place to place. Such repellents are also useful for the treatment of small containers housing sensitive electrical equipment that can be affected by the presence of the insects, their excreta, or their oötheca. Several highly effective materials are available for such purposes, e.g., 1,5a,6,9,9a,9b-hexahydro-4a(4*H*) dibenzofurancarboxaldehyde; tert-butylsulfinyl dimethyldithiocarbamate; 2-hydroxyethyl octyl sulfide; and octyl propyl sulfoxide; but they possess rather strong and sometimes offensive odors.

PROTECTION OF CROP PLANTS

Even though repellents have been demonstrated among several synthetic materials, in secretions of many species of insects, and in a number of plants, there have been no principles established for their use in the protection of crops in the field. The chemical identification and economical synthesis of potent repellents may make their use feasible as a control measure, either by themselves or in combination with other methods. Theoretically, repellents might be applied directly to or in the vicinity of crops to interfere with or mask the natural odorous attractants present and thus disorient or actually repel the insect. Repellents such as creosote have been used as barriers to the movement of crawling insects such as chinch bugs, *Blissus leucopterus* (Say). The usefulness of repellents in the protection of plants is largely unexplored.

Several feeding deterrents (not to be confused with repellents; see Chapter 12) have been discovered for different species of insects. Most of these are synthetic products, but several have been found in extracts of plants. The plant derivatives often come from resistant varieties of the host plant, but some come from closely related species that are unfavorable as hosts. For example, feeding deterrents extracted from resistant strains of corn, *Zea mays* L., greatly reduce feeding by larvae of the European corn borer, *Ostrinia nubilalis* (Hübner), and extracts from rose of Sharon, *Hibiscus syriacus* L., protect cotton squares from feeding by boll weevils, *Anthonomus grandis* Boheman. The detection and extraction of feeding deterrents from natural products has advanced the possibility of utilizing these materials in control programs. Feeding deterrents might be used alone to prevent damage to plants by insect feeding or to increase the effectiveness of other control measures. They might be applied to the host plants to discourage normal feeding, and portions of the plants, or a few strategically located plants, might then be resprayed or baited with attractants or feeding stimulants or both, containing toxicants, sterilants, or pathogenic organisms. The insects, although attracted to the plant, would be discouraged from feeding on plant tissue because of the deterrent and would instead feed on the attractive material containing the control agents.

PROTECTION OF FORESTS

There has been no practical use of repellents for control of forest insects. However, research on pine bark beetles (Scolytidae) has shown the presence of volatile resins that apparently cause the resistance of certain species of pine to bark beetle attack. Resistance or susceptibility of southern pines, *Pinus* spp., to attack by tip moths, *Rhyacionia* spp., also appears to be governed by the composition of oleoresins in the various pine species. Preliminary studies on other forest insects have shown promise for the isolation of repellents or feeding deterrents. There is need for expanded research on forest insect–host relationships, including the isolation and characterization of nonhost chemicals acting as repellents or oviposition and feeding deterrents. With this knowledge, it might be possible to use these chemicals or laboratory-synthesized substitutes for treating forested areas to repel destructive insects. Discovery of behavior-affecting chemicals would give plant breeders a screening technique for the selection of forest trees that produce these substances in a concentration great enough to prevent insect attack.

EVALUATION OF REPELLENT USE

Repellents have two principal advantages: since they need not kill the pest species, the best repellents have low general toxicity and may be used safely on man, beneficial animals, and food plants; and they can provide protection for an individual man, animal, or plant without the necessity of destroying a huge segment of the pest population, with all the expense, difficulty, and even hazard that this may involve. Repellents also have some disadvantages. Because the pest population is not destroyed, but is only held at bay, the host must be completely and continuously covered with the repellent to obtain protection. The repellents that protect man and animals are lost rapidly by abrasion, evaporation, and absorption through the skin, which necessitates retreatment at intervals of a few hours or days at most. The potential value of repellents, like that of other agents influencing insect behavior, warrants much additional research.

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CHAPTER 15

Sterilization

Sexual sterilization of insects was established as a practical means of control in the mid-1950's, when the screw-worm fly, *Cochliomyia hominivorax* (Coquerel), was eradicated from the West Indian island of Curaçao and from the southeastern portion of its range in the United States by the release of flies sterilized by exposure of the pupae to gamma radiation. Since then, exploratory studies with the method against other species of insects have sometimes been encouraging and sometimes discouraging. The most successful research on other species involved the tropical tephritid fruit flies. The melon fly, *Dacus cucurbitae* Coquillett, was eradicated from the South Pacific island of Rota in a pilot program involving the integration of a bait spray and sterile-insect releases. A low-level population of the oriental fruit fly, *Dacus dorsalis* Hendel, was also eliminated from the Pacific island of Guam by releasing sterile insects. Releases of sterile Mexican fruit flies, *Anastrepha ludens* (Loew), are now employed along the Mexico–California border area to prevent the establishment and spread of the insect in this area. Acceptable levels of control have been obtained in experiments with several other species, but practical development of the technique in these cases has not yet been achieved. The sterility technique will not be practical for controlling many insects, but it could play a prominent role in the control, and possibly the eradication, of some of the major insect pests.

The sterility principle can be applied in two ways: by rearing insects and sterilizing them for release and by using chemicals to induce sterility in the natural population. The basic concept by either approach is that the sexually sterilized insects mate with normal insects in the population, thus neutralizing their reproductive potential. If the number of sterile matings exceeds the number of normal matings to a sufficient degree, the population will decrease in each subsequent generation. If the number of sterile insects is maintained at a constant level through releases while the number of normal insects is declining, the ratio of sterile to normal matings will increase rapidly in successive generations. In almost all species, released sterile males will play a more important role than released sterile females. When chemical sterilants are used in baits to induce sterility in the natural population without releases, there will be no such increase in sterile:normal ratios in successive generations, since the percentage of insects feeding on the baits will presumably remain the same. Baits that attract both sexes to sterilants have a great potential advantage over insecticides, in that the reproductive capacity of the females that consume adequate quantities of the bait is eliminated as well by a chemosterilant as by a toxicant, and the males that feed adequately on the bait survive to mate with females that do not feed on it, thus destroying their reproductive capacity also.

The success achieved by an application of a chemical sterilant to the natural population, and any advantage in effectiveness that it will have over an insecticide, will depend on the ability of the sterilized insects to seek out, mate with, and further reduce the reproductive capacity of the normal insects. The sterile-insect release method has its greatest potential for eliminating or controlling pests when their populations are at a low level. The method is therefore especially advantageous when used in integrated programs in which the population has first been reduced by other methods.

DEVELOPMENT OF AUTOCIDAL CONTROL

The employment of an insect to destroy its own kind, or to bring about the self-destruction of the species, is known as autocidal control. Many methods of insect control utilize the behavioral patterns of the species, but the application of the sterility technique depends to a unique degree on the exploitation of the autocidal principle.

EARLY STUDIES ON MUTATIONS AND STERILITY

X Rays

In the late 1930's, consideration was first given to the hypothesis that if the male of the screw-worm fly could be sterilized without impairing their mating behavior, the sterilized males might be used to eradicate a natural isolated population, since the females mated only once. The sterilizing effect of x rays on insects had been observed as early as 1916, when it was demonstrated that adult cigarette beetles, *Lasioderma serricorne* (Fabricius), irradiated with x rays subsequently laid infertile eggs. About 10 years later, an increase in the mutation rate in *Drosophila melanogaster* Meigen was observed to follow x-ray treatment. This greatly stimulated mutation research, not only with *D. melanogaster*, but with other insects as well. Some of the mutations were lethal in the progeny, and, when adequate doses of radiation were used, males and females became sterilized. The sensitivity to x rays was not only species-dependent, but also varied according to the stage of development of the insect. When the males were subjected to ionizing radiation, the resulting sterility was attributed to dominant lethal mutations in the spermatozoa. These mutations proved to be the result of complex genetic injury in the sperm, which initiated a long series of developmental abnormalities, resulting in embryonic death. Therefore, the genetic changes in the sperm did not prevent penetration of the egg, but prevented the zygote from developing normally.

In 1950 it was found that when screw-worm pupae were irradiated with x rays within 2 days of adult emergence, a dosage of 2,500 R sterilized the males, but a dosage of 5,000 R was required to sterilize the females.

Gamma Rays

Prior to World War II, almost all irradiations were carried out by x rays, usually with medical equipment, although in a few instances gamma rays from radium were used. After the advent of the atom bomb and the availability of man-made isotopes, it became much easier and more convenient to irradiate insects with gamma rays. The isotopes most commonly used in gamma sources are cobalt-60, with a half-life of 5.3 years, and cesium-137, with a half-life of 30 years.

There is little difference between hard x rays (100 kV and up) and gamma rays in their biological effectiveness in treating insects. The advantage of gamma rays from cobalt-60 sources is that much larger volumes of material can be irradiated at one time, and cobalt sources are more economical to operate than x-ray equipment. In fact, the availability of cobalt-60 sources was an important factor in establishing the feasibility of the sterile-male technique for insect-population control.

The effects of x rays and gamma rays on the screw-worm were compared. No differences occurred when 6-day-old pupae were subjected to 5,000 R. The only deleterious effect was a decrease in the longevity of the adult males. In cage tests with different ratios of sterile males, untreated males, and untreated females, the males sterilized with 5,000 R competed almost equally with untreated males. These interesting and encouraging results stimulated additional studies with screw-worms and several species of tephritid fruit flies.

Chemosterilants

The discovery that certain chemicals produce a type of sterility in insects similar to that produced by radiation aroused wide interest in the potential use of such materials as control agents. These chemicals are called radiomimetic because many of their effects resemble, or "mimic," those of radiation.

Insect chemosterilants are chemicals capable of causing sexual sterility in insects, that is, preventing reproduction. They may act in any one of three principal ways. First, they may cause the insects to fail to produce ova or sperm. Antimetabolite chemosterilants act in this way. Antimetabolites are compounds that, when introduced into an organism, will elicit signs associated with the lack of a specific metabolite essential to cell development. Second, they may cause the death of sperm or ova after they have been produced. The third type of action, and the one most exploited up to the present time, is the induction of dominant lethal mutations, as exemplified by the alkylating agents. Alkylating agents are compounds capable of replacing hydrogen in an organic molecule with an alkyl group. In female insects such compounds prevent further development of the ova; in males (when administered at the proper stage of development) they often result in the production of normal numbers of live, fully active sperm bearing genetic defects that prevent the development of any zygotes formed by them. The third type of action is desired, because males thus sterilized are usually competitive with normal males in mating with available females in the population.

The action of alkylating agents and antimetabolites as insect sterilants was reported in the early 1950's, but the full potential of these chemosterilants as control agents was not generally recognized until the end of that decade, after the screw-worm eradication program had demonstrated the effectiveness of the sterility technique.

About 6,000 compounds have now been screened, and more than 300 have shown promise as chemosterilants. The effective compounds represent such diverse groups as the alkylating agents and their analogues, various antimetabolites, antibiotics, alkaloids, and organotin compounds.

PRACTICABILITY IN CONTROL OF SCREW-WORM

The success achieved in eradicating the screw-worm fly from the island of Curaçao in 1954 and from the southeastern United States in 1958–1959, by the release of insects sterilized with gamma radiation, is well known. Less well known is the fact that this achievement was the culmination of more than 20 years of research, often with negative results, directed toward that specific goal. It is desirable to call attention to the early work so that investigators working with other species will not become discouraged and abandon efforts because of the reversals they are likely to encounter. With this method, success depends on many ecological and behavioral factors which vary from species to species.

The possibility of controlling the screw-worm by introducing sterile males into a natural population was supported by several features of the life history, biology, and population dynamics of the species. Total numbers of the insect in a given area were relatively low. Further, since the insect was a tropical species, its range in the United States was greatly restricted during the winter months—a situation that reduced the population still further. A method of rearing the insect on an artificial medium consisting of ground lean meat, blood, water, and formaldehyde had been developed. Sterility had been induced by irradiation of the pupae with gamma rays, and sterile males had been shown to compete satisfactorily with normal males in mating with normal females, although they were not fully competitive.

The crucial requirement was to determine whether released sterile males would compete with normal males in nature. The first experiment, made on a small island ½ mile off the coast of Texas, demonstrated nothing. The next attempt was a release in an area of about 1,000 square miles in Florida. One side of the release area was along the coast, to provide some isolation. Again the release demonstrated nothing of any significance. The third effort was on Sanibel Island, about 2 miles off the west coast of Florida. Sterile flies released at the rate of 200 (about 100 males) per square mile produced 80% sterility in the egg masses laid by the native wild females within 2 weeks of the first release. After 3 months the natural population on the island was very low, but occasional fertile egg masses were found, probably from flies invading the island from the mainland. The need for evaluating the method on a completely isolated population of the screw-worm was indicated in this first encouraging field experiment.

The first completely successful field eradication experiment was conducted on the island of Curaçao off the coast of Venezuela. Following preliminary experiments, which induced less than 50% sterility in egg masses from native flies, sterile flies were released over the entire island at the average rate of 435 males per square mile per week. In 8 weeks the percentage of sterile egg masses rose to 100%, and no egg masses were found after 13 weeks.

The success of the Curaçao experiment demonstrated the potentiality of the method for the eradication of the screw-worm from the southeastern United States. Screw-worms had not occurred in that part of the country prior to the mass shipments of cattle into the area in 1933, and it was hoped that if they were once eradicated reinfestation could be prevented by suitable quarantine measures. However, the area in which the flies normally survived the winter included most of Florida, or about 50,000 square miles, and the development of methods to rear, sterilize, and release 4000 sterile males per square mile per week constituted a formidable research requirement (Figures 37–40). In the course of the eradication program, more than 50 million flies were produced each week, and more than 2 billion were released over a period of about 18 months in Florida and parts of Georgia and Alabama—an area of about 70,000 square miles. More than 40 tons of ground horse and whale meat were required each week to rear the larvae, and 20 aircraft were employed in the distribution of the sterile flies. The first releases, in the southern portion of the area, were begun in January 1958, and by February 1959—6 months after all areas had been receiving releases—the species appeared to be eradicated, although releases were continued until November 1959. The only recurrences of the species in the area have been small infestations, directly attributable to importation of infested animals; these have been quickly eradicated by treatment of infested animals and releases of sterilized flies.

FIGURE 37 Mass rearing of screw-worms. The white-roofed hangar and nearby buildings at Mission, Texas, house a plant where 100 to 150 million screw-worm flies were reared each week, for sterilization and release over the infested area of southwestern United States and adjacent areas of Mexico. (USDA photograph)

FIGURE 38 Mass rearing of screw-worm larvae in large vats. A mixture of ground meat, citrated beef blood, and water is piped into the vats and maintained at 37°C by electric heating elements below each vat. The racks containing the vats move along a monorail. (USDA photograph)

APPLICATION OF STERILITY PRINCIPLE

REARING, STERILIZATION, AND RELEASE OF INSECTS

Although a variety of approaches to the use of the sterility technique have been proposed, many of which hold great promise, the only approach of proved practical value is that of rearing, sterilizing, and releasing insects in numbers that will overwhelm the natural population.

The use of sterile-insect releases as a means of population control may be considered for practical application the following situations: (1) to control well-established insect populations when the species occurs in small numbers at certain periods in the population density cycle and if it is practical to rear large numbers of the insect at reasonable costs; (2) to eliminate incipient infestations of an insect or to prevent the spread of an established insect; and (3) to help control or eliminate well-established insect populations that have first been reduced to manageable levels for sterile releases by employing other methods of control, such as insecticides, cultural measures, or any other methods that are more efficient when the natural population is high. The population density level at which sterile-insect release is more efficient than the continuation of other methods is governed by a number of factors pertinent to each insect problem.

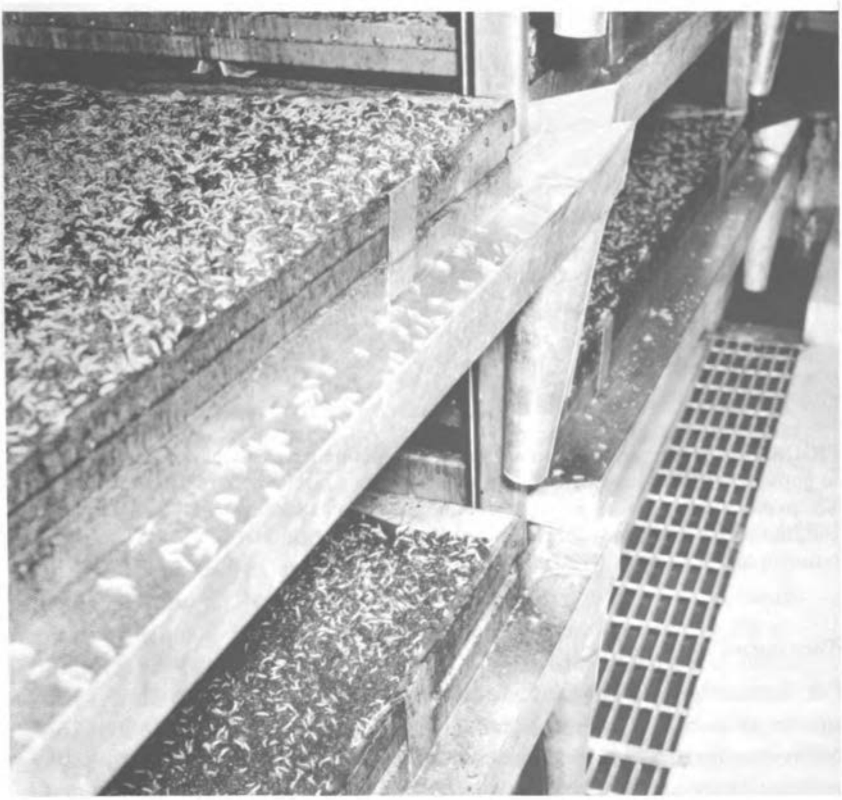

FIGURE 39 Mass rearing of screw-worms. Fully grown larvae migrate from the medium into a trough and fall through a funnel and grating into a water channel under the floor, which carries them to a separator and dryer. (USDA photograph)

FIGURE 40 Mass rearing of screw-worms. The mature larvae are placed in trays of sawdust to pupate. Every 8 hours the trays are emptied onto a machine that screens out the sawdust. The pupae and any remaining larvae are then placed on a moving belt; pupae remain on the belt, but larvae are driven by lights to a collecting trough at the edge of the belt and are returned to the sawdust. (USDA photograph)

Necessary Characteristics of Species To Be Controlled

For the sterile-release method to be successful, the first necessity is that the species to be controlled can be reared economically in greater numbers than occur in nature in the infested area at the time. The natural population may be reduced by insecticides or other methods, however, before releases are made. For most species it will be necessary to rear millions of insects each week, since there are few species which would be seriously affected by releases on a smaller scale. Rather simple food requirements facilitate mass rearing, but synthetic diets for even the most fastidious species may be developed by painstaking and imaginative research. For a few species such as the tsetse flies, *Glossina* spp., there may be situations where it would be feasible to collect the insects for sterilization and release in sufficient numbers to avoid the necessity of rearing.

In estimating the ability to rear insects in adequate numbers, it is necessary to know how many individuals will be needed per unit area and per unit of time for any given situation. Methods for determining the absolute abundance of insects in an area are sadly lacking. Much research is needed to develop such methods. From the scanty information at hand it appears that the actual numbers of many species at the lowest point in their seasonal cycles of abundance are not as large as has usually been assumed.

It is essential that the released insects do not in themselves constitute a nuisance or source of injury. The release of overwhelming numbers of insects such as house flies, *Musca* spp., and cockroaches (Blattidae) would not be readily accepted in most locations. It would be impractical to release large numbers of insects that serve as vectors of diseases of man, animals, or plants; however, if only the female insects carry the disease, as in the case of mosquitoes (Culicidae), sterile males could be released. Insects that feed on crops in the adult stage could be released only in numbers that would not produce more injury than could be economically sustained. Such species might be released at times when the crop plants are not susceptible to injury or in such small numbers that they do not cause economic damage but still adequately overflood a low natural population.

The sterile-insect release method will probably be impractical against most established populations of prolific species or against species that are of little economic significance. It would probably prove impractical to use the method against insects that appear sporadically in large numbers, such as floodwater mosquitoes, *Aedes sticticus* (Meigen), since it would be necessary to incur the cost of constant mass production to be ready for releases at the unpredictable times of natural outbreaks.

The method will achieve maximum effectiveness only with species in which the males and females mix over a considerable area before mating occurs. Insects that have a greatly restricted range of movement may pose problems of achieving adequate distribution and placement of sterile insects in the required number to compete satisfactorily with the normal insects in different parts of the total area. For example, in attempting to control or eradicate scale insects by releasing sterile individuals, we could anticipate difficulty in achieving adequate distribution of the released insects even on a single tree. In order to achieve complete population control of an insect, it is important that all segments of the population are adequately overflooded with the sterile insects.

From a theoretical standpoint, multiple matings by females need not reduce the effectiveness of the method, and, in fact, the females of the melon fly (which was eradicated from the island of Rota by this method) are polygamous. The influence of multiple matings by the females must, however, be determined experimentally for each species.

It is necessary to be able to sterilize the insects without too serious effects on their vigor, longevity, behavior, or mating competiveness. However, if all other factors are favorable, research should be vigorously pursued to achieve satisfactory sterility by some type of irradiation, chemicals, hybridization, or cytoplasmic incompatibility (see Chapter 9).

Facilities Required

Radiation Although many different sources of ionizing radiation could be utilized for the sterilization of insects, the most useful from a practical point of view are x rays and gamma radiation. These two types can be produced by a variety of x-ray machines and gamma sources. For instance, x-ray equipment ranges from low-energy machines, such as those in the 50- to 300-KeV range, to 2-MeV generators. Typical doses from a 300-keV machine (maximum current 10 mA) with no filter reach 25 R/min at 1 m. At closer distances, the exposure rates follow the inverse square law to a level around 1,500 R/min near the tube. With a 2-MeV x-ray generator, exposure rates exceeding 20,000 R/min are possible close to the tube face. The LET (linear energy transfer) spectrum of 2-MeV x rays is comparable to that of cobalt-60. Modern versions of all types of x-ray machines can be operated on an almost continuous basis. However, they do require a source of electrical power, a requirement that limits their mobility under some circumstances.

Gamma-beam units, such as those employing cobalt-60, constitute the simplest and most useful sources of radiation. Available cobalt sources vary from simple rods, which can be raised from a lead shield to irradiate material in an open room, to sophisticated push-button machines with protected annular arrangements of cobalt-60 rods into which targets can be lowered for exposure. A typical simple unit contains 1,500 Ci (or greater amounts to 3,000 Ci) in lead shielding with an aperture subtending 35° in both the horizontal and vertical directions. The source can be lowered to a safe position following irradiation. Exposure rates at 1 m (with 1,500 Ci cobalt-60) are about 25 R/min and follow the inverse square law at distances greater than 40 cm. Exposure times can be extended to many days, with total doses amounting to hundreds of thousands of roentgens. Small targets can be exposed at rates as high as 2,500 R/min. The radiation from cobalt-60 is essentially monoenergetic with LET distribution between 0.2 and 1 keV/μ.

Chemosterilants The facilities required for sterilizing large numbers of insects with chemicals will vary with the species and method of application. For species that can be sterilized in the pupal stage, all that will be necessary will be large vats containing the chemical in which the pupae can be immersed for fixed periods of time, although with some species it may be necessary to draw a vacuum in the vat to assure penetration of the pupae by the chemosterilant solution. If the species can be sterilized in the larval stage, the larval rearing containers can probably be used for the chemosterilant treatments.

Sterilization in the adult stage will generally require more elaborate facilities for holding large numbers of active insects without the injuries usually caused by overcrowding. For some species it may be possible to cause the adult insects to sterilize themselves as they emerge from the pupae, by forcing them to crawl through a medium of treated sand, sawdust, or vermiculite, through treated glass tubes, or between treated plates. Such insects could be safely released after a predetermined time shortly after emergence, and little holding space would be required. Sterilization of the insects by feeding them a treated diet (the method which in many species provides the maximum degree of sterility with the least other injury) will require batteries of containers for holding the insects under optimum conditions before, during, and after treatment.

All methods will require facilities for handling the chemosterilants without hazard to personnel. Adequate working space is a necessity, since crowded conditions foster accidents. Hoods for use when handling concentrated formulations should be available, all areas should be well ventilated, throw-away containers should be used wherever possible, and facilities for decontaminating other vessels, often in acid baths, should be provided, as should masks, gloves, and protective clothing. Emergency showers should be readily available.

STERILIZATION OF INSECTS IN A NATURAL POPULATION

There are many species of insects that are not suited to control by the rear-and-release method. Some are not adaptable to laboratory rearing. With others the numbers required to overwhelm the normal population would be too enormous. With still others the released insects would themselves be dangerous, destructive, or annoying. To control or eradicate such species it would be highly advantageous to be able to induce sterility chemically in a large proportion of the existing natural population in such a way that the sterile males would mate with and thus render infertile the females that escaped the sterilizing chemical.

Chemosterilants should have a distinct advantage over insecticides for the control or eradication of some species. The principal advantage of a chemosterilant over an insecticide may be explained briefly by assuming that a method of application is available that will expose 90% of the insects in the population to the chemical. If 90 males out of 100 and 90 females out of 100 are killed by an insecticide, for example, the 10 females that escape the treatment will mate with the 10 males that escape, and there will be 10 fertile females to produce the next generation. However, if 90% of each sex are exposed to a chemosterilant, 90 females out of 100 will be sterilized, and, in addition, the 10 females that escaped treatment will be subjected to mating competition by 90 sterile males as well as 10 normal males. From this ratio it would be expected that only one normal female would mate with a normal male and thus be available to produce the next generation.

Necessary Characteristics of Species To Be Controlled

The chemosterilant technique should be effective in the control of most species in which the males and females that are produced over a sizable area mix thoroughly before mating takes place. Chemosterilants would lose much of their advantage over insecticides in the control of species in which both sexes remain near the site of emergence until after mating has taken place.

All the chemosterilants that are presently of promise for practical insect control are mutagenic agents. For this reason they can be used only in ways that will avoid all contact between them and man or beneficial animals. Therefore, another essential characteristic of any species to be controlled by chemosterilants is that it have behavioral patterns that permit it to be treated without exposing man or beneficial animals. Species that are drawn in large numbers to baits or other attractants should be particularly susceptible to this method of control.

Methods of Application

All the promising chemosterilants are effective when ingested. The use of baits is therefore one of the most obvious methods of application. To achieve control with safety, a high proportion of the population must feed on the bait when it is displayed in a way that will not endanger other species. Some chemosterilants are effective by tarsal contact. It may be possible to use these to sterilize insects that are attracted to lights or sex attractants, by luring them to rest on treated surfaces. A few species may be susceptible to control through application of the chemosterilant to the larval medium, when they breed in places where this can be done with safety.

POTENTIALS FOR APPLICATION OF AUTOCIDAL CONTROL

The sterility methods for insect population control involve two different procedures. They affect population trends in different ways. The basic requirements for their effective and practical application are different. One of the sterility procedures, which has been employed successfully for eradicating and controlling populations of the screw-worm and certain tropical fruit flies, involves the mass production, sterilization, and release of insects that compete with the fertile individuals in the population. The second procedure involves the sterilization of a portion of the natural population. If the sterilization method does not adversely affect mating competitiveness of the insects, it can nullify the reproductive capacity of a like percentage of the individuals of the population that escaped sterilization. The total effect on reproduction is therefore much greater than would be obtained by killing an equal number. The basic concepts involved in insect-population suppression by various methods of control should be thoroughly understood to appraise the merits and limitations of each system when employed alone or when used in combinations. These basic concepts must be considered in relation to the biology, behavior, population dynamics, economic importance, and other factors pertinent to the particular insect to be controlled. The differences in the effect on insect-population trends achieved by the different methods of control can be illustrated best by establishing hypothetical insect-population models.

TREND OF UNCONTROLLED INSECT POPULATION

To begin with, we will establish a hypothetical insect-population model that depicts the assumed normal trend of an untreated population starting from a low level in the density cycle. It will then be possible to calculate the theoretical effect on population increase achieved by different methods of control. The rate of population growth of an uncontrolled insect varies with the inherent reproductive potential of the species, the nature and intensity of natural hazards in the environment, available food supplies, and many other factors. Although some insects, such as tsetse flies, have a low increase potential, many others have the capacity to produce hundreds of eggs or larvae. Such insects could conceivably increase at a very high rate. However, the maximum reproductive potential is never realized, because of the many natural environmental hazards that limit survival. A 10-fold increase rate for an uncontrolled population, starting from a low level in a favorable environment, should be a reasonably realistic increase rate for many of our economic insect species. The trend of such an uncontrolled population through three generations is shown in Model 1. It is unlikely that an insect population will increase at a constant rate each generation, and, as the population increases, the survival rate will tend to decline because of population density-dependent factors. However, all natural population density-dependent factors are ignored in the hypothetical population models, in order to clearly evaluate the capabilities of the various methods of control to be considered.

MODEL 1 Trend of an Uncontrolled Insect Population Increasing at a 10-fold Rate per Generation

Generation	Number of Insects in Population
1	1,000,000
2	10,000,000
3	100,000,000

It is apparent from this model that an insect population, even though increasing at a low rate in relation to the maximum potential, can still reach a high density within a few generations. It would require 90% control above natural hazards to keep the hypothetical population from increasing.

EFFECT OF INSECTICIDES ON POPULATION TRENDS

Although we are principally concerned here with the sterility methods of insect control, we might be in a better position to analyze the merits and limitations of the two sterility methods critically if we first consider the characteristic features of the conventional insecticide method for controlling insect populations. Model 2 shows the theoretical effect of a high level of kill if an insecticide is applied uniformly to the entire population each generation. The survivors of each generation are assumed to show a 10-fold increase in progeny.

With the conventional method of insect control with insecticides, the destruction of 98% of the population would have an immediate and dramatic

MODEL 2 Trend of an Insect Population Subjected in Each Generation to 98% Kill with Insecticides

	Number of Insects in Population		
Generation	Before Treatment	After Treatment	Number of Progeny
1	1,000,000	20,000	200,000
2	200,000	4,000	40,000
3	40,000	800	8,000
4	8,000	160	1,600
5	1,600	32	320
6	320	3	30
7	30	< 1	0

impact on the total population. The initial population numbering 1 million would be reduced to 20,000 by the first treatment. This is why good insecticide treatments are so valuable for the immediate control of insects that affect our health and welfare. However, as the population declines, the insecticide method becomes less and less efficient in terms of the number of insects destroyed. If eradication is the objective, more treatments are required to eliminate the last 1% than are needed to destroy the first 99%. Thus, unless insecticide treatments kill 100% of the population, the use of insecticides becomes highly inefficient in terms of the number of insects killed in the final stages of eradication programs. This is borne out by practical experience. Insecticides, in terms of the number of insects killed, may also be highly inefficient when they are employed routinely to prevent population buildup.

EFFECT OF STERILIZATION OF INSECTS IN A NATURAL POPULATION

We may now consider the characteristic trend of an insect population subjected to chemical sterilization instead of killing. It is assumed that the chemosterilant causes irreversible sterility in both sexes of the exposed insects without adversely affecting sexual vigor or behavior. The results are shown in Model 3.

The sterilization of 98% of the initial population would immediately reduce the reproductive potential of the total population by 98% and would also result in 49 sterile insects for each fertile insect in the population. Thus, only 400 of the 20,000 untreated insects (1 in 50) would be expected to encounter fertile mates. With a 10-fold increase for those that did encounter fertile mates the progeny would number 4,000. If insecticides are used, as shown for Model 2, in the first generation the 20,000 survivors of the treatment would produce 200,000 progeny, or 50 times more than would result from the chemical sterilization procedure shown in Model 3. Another treatment with a chemosterilant in the second generation would have the same proportionate effect as in

MODEL 3 Trend of an Insect Population Subjected in Each Generation to 98% Sterilization

	Number of Insects in Population			
		After treatment		
Generation	Before Treatment	Sterile Insects	Fertile Insects	Number of Progeny
1	1,000,000	980,000	20,000	4,000
2	4,000	3,920	80	0

the first generation. This would mean that 80 untreated insects would be competing for mates with 3,920 sterile insects. Theoretically, less than two would find fertile mates, and no progeny would be expected.

According to Models 2 and 3, the sterilization of a high percentage of both sexes of an insect population would have a much more drastic effect on the reproductive potential of the population than the conventional method of killing the same percentage of both sexes of the population. However, when populations are low, the sterilization method applied to the natural population has the same basic limitation as the killing method. It would require just as much material and the same cost to sterilize 98% of 4,000 insects in the second generation as would be necessary to sterilize 98% of the original population of 1 million. Thus, the only basic difference in the killing and sterilization methods is that the sterilization method is theoretically vastly more efficient. The treatment of the natural population by the chemosterilant approach to insect control results in two separate and independent actions that lead to population suppression. The first action is chemical; the second is biological. The insects exposed to the chemical cannot reproduce, because of the effect of the chemosterilant. But they in turn become biological organisms that nullify the reproductive potential of a like percentage of their potentially fertile siblings.

EFFECT OF RELEASE OF STERILE INSECTS ON POPULATION TRENDS

The best-known sterility involves the mass production, sterilization, and release of sterile insects capable of competing with fertile individuals of their own kind in the natural population. The characteristic effect of this method of control on population trends is shown in Model 4. The release of 49 million sterile insects among a natural population consisting of 1 million fertile insects would provide a sterile-to-fertile ratio of 49:1. This, theoretically, would nullify the

MODEL 4 Trend of an Insect Population Consisting of 1 Million Individuals when Subjected to the Sustained Release of 49 Million Sterile Insects

Generation	Natural Fertile Population	Released Sterile Population	Ratio of Sterile to Fertile	Number of Progeny
1	1,000,000	49,000,000	49:1	200,000
2	200,000	49,000,000	245:1	8,130
3	8,130	49,000,000	6,027:1	0

reproductive capacity of 98% of the natural population. With a 10-fold increase for those that encountered fertile mates, the total progeny would number 200,000. This would have the same effect as 98% kill with insecticides during the first generation.

However, the same number of sterile insects released in the second generation would have a much greater effect than the use of insecticides in the second generation. The ratio of sterile to fertile would increase to 245:1. This would provide 99.6% control of reproduction. The expected decline in the natural population would then lead to the overwhelming ratio of 6,027 sterile to 1 fertile when 49 million sterile insects are released in the third generation. Less than 2 of the 8,130 natural fertile population would be expected to mate, so theoretical elimination would be achieved. The method of inducing sterility in the insects before release may be physical (gamma radiation), chemical (chemosterilant), or genetic (hybrid sterility) (see Chapter 9). However, the effect of the released sterile insects is entirely biological.

The characteristic effect on natural population trends resulting from sterile-insect releases is markedly different from the effects of insecticide or chemical sterilant treatments. The significant feature of the sterile-insect release method is that it is highly inefficient when the natural population of an insect is high, but it becomes increasingly more efficient as the natural population declines and the ratio of sterile to normal insects increases. This is in contrast with the characteristic effect of most other methods of insect control including the use of insecticides and the application of chemosterilants for sterilizing the natural population.

Recognition of the relative efficiency of two such contrasting methods of insect-population suppression, depending on the natural population density, should eventually lead to more effective and more practical insect control and eradication. These fundamental principles of insect-population suppression are not yet fully appreciated by the scientific community. However, we next consider the great advantage achieved by combining two such systems for the suppression of an insect population.

CHARACTERISTIC TRENDS OF INSECT POPULATIONS SUBJECTED TO AN INTEGRATED PROGRAM OF INSECTICIDE TREATMENTS AND STERILE-INSECT RELEASES

The potential advantage of the integration of insecticide treatments and sterile-insect releases is shown in Model 5. We will retain the same basic assumptions established for previous hypothetical models. The insecticide treatments are assumed to destroy 98% of the original parent population. The initial sterile-insect releases will then be made at a level that provides a ratio

MODEL 5 The Combined Use of Insecticides and Sterile-Insect Releases for the Elimination of an Insect Population

Generation	Initial Insecticide Treatment–98% Kill	Fertile Population Remaining	Sterile Population Added	Ratio of Sterile to Fertile	Number of Progeny
1	1,000,000	20,000	980,000	49:1	4,000
2	No insecticide treatment	4,000	980,000	245:1	163
3	No insecticide treatment	163	980,000	6,027:1	0

of 49 sterile to 1 fertile. The insects that survive and encounter fertile mates are assumed to produce 10 progeny.

By noting the results of the combined program in comparison with insecticides alone (Model 2) and sterile-insect release alone (Model 4), it is possible to appraise the potential advantage of the combined integrated program in comparison with each method employed alone. Treatments for seven generations would be necessary with insecticide treatments alone at the 98% control level to achieve theoretical elimination of a starting population of 1 million insects. Sterile-insect releases alone at the level of 49 million each generation would require the production and release of 147 million sterile insects to achieve theoretical elimination in three generations. However, the requirements for theoretical elimination by integrating the two methods would be an insecticide treatment for only one generation and the production and release of only 2,940,000 insects over three generations. If we assume that the costs of control by the use of insecticides alone and by the use of sterile-insect releases alone are the same, we can postulate that a combined program at the percentage control levels established would cost only about one fifth as much as either system employed alone.

The use of sterile-insect releases combined with an insecticide control program is cited as an example to show the advantage of combining two independent systems of control that have contrasting efficiency potentials, depending on the natural population density of the pest. However, a combination of chemosterilant treatments to sterilize insects initially when the natural populations are high, followed by sterile-insect releases, would theoretically be even more efficient than the insecticide–sterile-insect release combination. In this case, using the same basic insect-population model, the release of only about 500,000 sterile insects would be adequate to eliminate the population following treatment with a chemical sterilant in the first generation to achieve 98% sterility of the natural population. Other systems of insect control, including insect pathogens, cultural measures, or the mass releases of parasites and predators, might be integrated with sterile-insect releases for equally effective and perhaps even more desirable results. However, every insect problem has distinctive features that must be investigated and related to the fundamental principles outlined above. Many factors must be considered in appraising the merits and limitations of the sterility method, as well as any other method, of insect-population suppression.

STERILIZATION METHODS

RADIATION

Stage of Insect Irradiated

Effective use of radiation-induced sterility in population control requires that the insect be rendered sterile without affecting its ability to live, mate, and carry on normal functions—except reproduction. The best stage to irradiate depends upon the insect studied and on the type of sterility required.

Irradiation of eggs usually prevents hatching or induces death in the larvae. The larval stage is very radiosensitive, and irradiation in this stage (or in the young pupae) is almost always accompanied by death prior to the adult stage, or by the induction of developmental abnormalities and the emergence of debilitated adults. If vigorous adults emerge, they may not be sterile. The tolerance of the pupae to radiation increases with age, and the older pupae are usually sterilized with minimal doses without affecting the adults severely (at least in the Diptera). It is probable that this change in radiation response coincides with the completion of mitotic proliferation of the imaginal tissue masses, since the adult structures are mostly complete in older pupae.

In most insects the pupal stage is the easiest to handle during irradiation, and often the dose of radiation required to produce sterility is the same or lower than that required to produce sterility when the adults are treated. Many adult insects can withstand radiation doses far in excess of the sterilizing dose without obvious effects on life-span and vigor.

It should not be assumed, however, that an organism that successfully completes development after irradiation is necessarily normal. Significant reductions in life-span, changes in behavior, and reduced ability to compete are sometimes found. The detrimental side effects detected will depend largely on the insect studied, the stage treated, and the investigator's ingenuity in measuring subtle differences.

The type of sterility produced is determined largely by the type of cells present in the testes when the male insects are exposed to radiation. In males, at least three different kinds of sterility are possible—dominant lethal mutations in the sperm, aspermia, and sperm inactivation. At certain life stages some male insects possess an assortment of reproductive cells (spermatogonia, spermatocytes, spermatids, and mature sperm). Others have mostly one kind of germ cell in their testes at any given stage. Each cell type differs in radiosensitivity and in the probability of surviving the radiation treatment. Consequently, irradiated males can exhibit several kinds of sterility, depending on the stage irradiated and the content of the testes. Sometimes the sperm transferred to the females will contain dominant lethal mutations. In some males the process of spermatogenesis is interrupted by the radiation treatment, and the males eventually become aspermic.

For species in which the females are polygamous or require sperm to remain monogamous, the sterile males must transmit sperm containing dominant lethal mutations that are competitive with the sperm contributed by normal males. The sterile males should contain a sufficient store of mature sperm or spermatids at the time of irradiation to last through the number of matings normally experienced by the males in the field. This type of sterility can also be used with monogamous species. However, males that contribute immotile sperm or no sperm at all might be equally effective, providing the act of copulation is sufficient to prevent the females from further matings.

Modifying Effects of Gases on Radiosensitivity

The biological effects of ionizing radiation depend on the gaseous environment during the radiation treatment. Gases such as oxygen or nitrous oxide enhance the amount of biological damage, but a vacuum or gases which produce anoxia (nitrogen or carbon dioxide) decrease the amount of damage produced by radiation. However, no gas offers complete protection against radiation treatments.

In practice, insects are generally irradiated in air. Once the sterilizing dose in air has been determined, the effect can be reliably repeated only when future treatments take place in the same environment. Thus, the atmosphere surrounding the insects during irradiation must be controlled to assure that they do not become anoxic. However, studies have not shown that gases offer any hope of protecting the insect against the detrimental side effects of radiation without affecting the level of sterility produced. If the radiation treatment is delivered in a protective gas, greater doses are required to produce sterility, and somatic damage would thus increase proportionately. Tissues that differ in free oxygen availability might be expected to respond differently. This area in radiation entomology is virtually unexplored.

CHEMICALS

Almost all chemosterilants are effective when given in the food of the adult insects; some, but not all, are also effective by tarsal contact or by topical application; and a few are effective when used in the larval medium or when applied to the pupae. Most of the compounds produce the maximum sterilizing effect with the least undesirable side effects when given in the food. With some species the sterility is permanent; in others it is not. With many chemosterilants the pH of the diet is important; e.g., aziridine compounds lose effectiveness rapidly in acid media, but neutral and basic baits remain effective for several weeks. Some chemosterilants may react rapidly with protein diets and lose effectiveness quickly. The food must be sufficiently attractive to overcome any repellency caused by the chemosterilant.

Chemosterilants that are effective by tarsal contact may be used to sterilize insects that walk on treated surfaces. The compounds now available require exposure of several minutes up to several hours on glass surfaces treated at 0.1 to 2.0 g/m^2. Deposits are usually less effective on wood or paper than on glass. Such compounds could be used in connection with light traps or sex lures to sterilize insects in the natural population. Many of the compounds that are effective by tarsal contact may also be applied to the insects as sprays or dusts.

Some species of insects, e.g., mosquitoes, can be sterilized by chemicals added to the larval medium. Usually, however, high concentrations are required and excessive mortality results, since the chemicals attack other developing cells as well as the gonads. Other species, e.g., the Mexican fruit fly, can be sterilized by dipping the pupae in a solution of the chemosterilant or by applying the chemical as a spray or dust. The sterilizing action may be caused, at least in part, by the contact of the newly emerged adults with the treated pupal cases. The pupal stage is the most convenient to treat for field releases, since pupae are inactive and millions of them can be handled in a small space and with simple equipment. Unfortunately, many species are refractory to treatment in the pupal stage, and more research is needed on methods to bring the chemicals to the target cells in adequate concentrations without causing excessive mortality.

MASS REARING

The use of released sterile insects as a means of population control will usually require the rearing of large numbers of the species under artificial conditions. The rearing methods must be suitable for the production of millions of insects each week, since there are few species that would be seriously affected by releases on a smaller scale, even after their numbers had been reduced by insecticides or other means, and even when the method might be employed to prevent the establishment and spread of incipient infestations.

Rearing insects by the million would not seem to pose many problems, especially if the species are characterized by the production of a large number of eggs per female, a short life cycle, and relatively simple food requirements. Some species, including many important economic pests, at first seem to be completely unsuited to mass production, in the light of our present knowledge. Even these may yield to painstaking and imaginative research, particularly if they possess the basic desiderata of high fecundity and short life cycles. Research toward mass production must emphasize the development of (1) foods or rearing media that can be thoroughly standardized and prepared from cheap and abundant raw materials (chemically defined diets are preferable); (2) techniques for extracting all stages from their media; (3) techniques enabling the insects to tolerate crowding, since economy of space will be essential; (4) full information on the chemical and physical stimuli controlling mating and oviposition; (5) rearing-room isolation and use of disinfectants to avoid devastating losses attributable to diseases; and (6) maximum automation. Rearing methods must be dependable, because any failure could jeopardize the success of a large control program. Costs can be balanced against expected benefits.

The maximum rate of progress in the development of improved rearing methods should result from use of large numbers of adult insects to permit rapid selection of individuals with desirable characteristics, and by dense loading of larval media with eggs or larvae to the point where the size and number of those that mature are affected. Loading to capacity will help reveal nutrient or physical deficiencies and minimize the amounts of potentially toxic preservatives required to prevent bacteria and fungi from taking over a larval medium.

The quality of the insects produced must be evaluated through more than one generation to reveal latent harmful effects that might at first be obscured by the carry-over of nutrients from a previous generation fed on natural hosts.

Regulation of temperature, humidity, and light conditions that permit production at maximum speed consistent with quality of the insect produced will reduce equipment and manpower requirements and help maintain uniformity in the medium. The use of freshly prepared medium for eggs at time of hatch will minimize deterioration of the food, as well as the loss of eggs or larvae, and will increase the turnover rate in the production line.

The maintenance of good sanitation and disinfection of equipment with chemicals or heat are essential to any rearing program and can minimize the need for harmful amounts of preservatives in larval media.

Behavioral patterns of many species of insects may change on colonization. Some such changes may be unavoidable if the species is to be reared in overwhelming numbers. Constant surveillance must be maintained, however, by tests in the field or large outdoor cages, or in both, to be sure the colonized strain has not degenerated below the point of practical use, so that required corrective action can be taken, if necessary, by adding wild strains with superior qualities to the laboratory strain.

MASS HANDLING FOR STERILIZATION

Holometabolous species of insects are usually irradiated in the late pupal stages; hemimetabolous spieces are usually irradiated in the last nymphal instar or sexually immature adult stage. Nymphs or adults may require prior inactivation by chilling or anesthetization.

Most pupae, whether in cocoons or naked, must be protected from abnormal compression, desiccation, and concussion. Most naked pupae require delicate handling during sifting, pouring, and transportation. Densely packed pupae, particularly those of small size, require forced aeration to avoid anoxia and consequent reduced effectiveness of the dosage if the irradiation process, including prior time in bulk, extends more than a few minutes. Metabolic heat in some pupal masses as shallow as ½ inch, particularly if it occurs late in the pupal period, can accumulate to lethal levels, injure survivors, and also increase the danger of anoxia. Heat in the center of the pupal mass, by creating different development rates within the mass, also can spread the emergence period. Both overheating of pupae and overcrowding during emergence may produce crippled adults. Where pupae are produced daily but irradiated less frequently, different age lots can be programmed, by exposure to appropriate temperatures, to emerge on scheduled dates.

Chemosterilants may be applied as pupal dips, included in water or food for larvae or adults, or applied as sprays or aerosols to adult insects. They may be used as residues on surfaces around strong attractants or on materials which adult insects must crawl over or through as they emerge from puparia or cocoons. Dosages of chemosterilants may be more difficult to control accurately than dosages of radiation.

MEASUREMENT OF EFFICIENCY

Cross-mating of sterilized males with normal virgin females and normal males with sterilized females is necessary to determine the effectiveness of sterilizing treatments. To establish the minimum effective dosage that will produce irreversible sterility in the males, the males must be given periodic access to young, virgin, normal females.

Tests using different ratios of sterile to normal insects will measure the effect of the treated insects on reproduction in a mixed population. The tests should include several overflooding ratios of sterile to normal pairs in cages; eggs should be collected and hatching rates should be compared with those of normal matings throughout the life-span. Sterile and normal insects of various ages should be compared; sterilized males might be competitive at one age but not at another, and any retardation of sexual development in the sterilized individuals would enable the normal insects to mate first.

However, such ratio tests in cages may not accurately indicate sexual aggressiveness or searching and foraging ability in nature. In some species male aggressiveness is so pronounced that female mortality is high in the presence of excess numbers of males; in such species comparisons of mortality rates among females confined with large numbers of sterile or normal males provide a quick measure of the effects of sterilization on this characteristic.

Additional observations to evaluate the effectiveness of the sterilizing treatments should include periodic tests to determine the number of females that can be inseminated by single males. The spermathecae of the females must be dissected to determine the quantity of motile sperm transmitted by the males; observed copulation cannot be accepted as positive evidence of insemination.

If good means of recovery and identification are available, simultaneous field releases of marked sterile and normal insects can be made to measure dispersal and longevity.

SUSCEPTIBILITY RANGE

Species vary in their susceptibility to sterilization, more so with respect to radiation than to chemosterilants. Males are often more susceptible than females. Some male Diptera are sterilized at dosages as low as 2,000 R, which have relatively little effect on their vitality. However, some Lepidoptera require dosages of several hundred thousand roentgens, which produce high mortality and weak survivors. Some Coleoptera are intermediate in susceptibility to sterilization by irradiation but are difficult to sterilize without adverse side effects.

All tested species have proved susceptible to chemosterilization in some degree. The list now includes 15 species of muscoid flies, 6 species of mosquitoes, 6 Lepidoptera, 5 Coleoptera, 2 Hymenoptera, 2 Hemiptera, 1 Orthoptera, 3 mites, 1 spider, and 2 nematodes. However, it is difficult to secure satisfactory sterilization of some species. The boil weevil, *Anthonomus grandis* Boheman, for example, has not been sterilized with either radiation or chemicals without undesirable side effects such as early mortality, reduced vigor, or aspermy during the later portion of the active period of the males.

EFFECTS OF STERILIZATION ON SEXUAL BEHAVIOR

MATING CAPACITY AND COMPETITIVENESS OF STERILIZED MALES

Many species of insects, particularly among the Diptera, show no reduction mating capacity following sterilization by either radiation or chemicals; that is, single males caged with excess numbers of virgin females will inseminate equal numbers, whether sterilized or normal. Sterilized males of a few species show some reduction in mating capacity, and in such species radiation usually causes greater reductions than do chemicals. However, in some species the sterilized males may retain full capacity for noncompetitive mating but may be unable to compete for females on equal terms with normal males. Again, in such species, radiation usually causes a greater loss of competitiveness than does chemosterilization. In a few species, e.g., the house fly, *Musca domestica* (Linnaeus), and the screw-worm fly, the males sterilized with certain compounds are actually more competitive than normal males; i.e., when sterile and normal males compete for normal females, the ratio of sterile eggs to normal eggs exceeds the ratio of sterile males to normal males.

EFFECTS ON FEMALES OF INSEMINATION WITH DEFECTIVE SPERM

Normal females mated to males sterilized by radiation or radiomimetic chemicals usually lay normal numbers of eggs, but the eggs generally fail to hatch. Sometimes the lethal mutations carried by the sperm do not cause the death of the progeny prior to hatching but cause death in the larval or pupal stage. However, the evaluation of the treatment on the basis of the proportion of eggs that fail to produce mature progeny introduces the possibility that other factors causing larval mortality will distort the results.

Females that normally mate only once will rarely mate more than once when inseminated by males sterilized by radiation or radiomimetic chemicals, at least in the species that do not develop aspermy near the end of adult life.

Females sterilized by high dosages of radiation or chemicals may fail to oviposit. At lower dosages they may deposit the eggs that were in mature follicles at the time of treatment, which do not hatch, but fail to develop a second clutch of eggs.

EFFECT OF MULTIPLE MATINGS BY FEMALES

The females of many species of insects mate more than once; the effect of such multiple matings on the susceptibility of the species to control by the sterile-male technique must be determined by research on each individual species. In theory, there is no reason why a ratio of, for example, 9 sterile males to 1 normal male should not produce 90% sterility in the females, as long as 9:1 ratio can be maintained for all the matings. However, in some species, such as the yellow fever mosquito, *Aedes aegypti* (Linnaeus), and the boll weevil, matings with normal males have more influence than mating with sterile males; i.e., females mated to a sterile male, then to a normal male, lay all normal eggs, but females mated to a normal male, then a sterile male, lay some normal and some sterile eggs. One species with females that mate more than once, the melon fly, has been eradicated from the small island of Rota in the South Pacific by overflooding with males sterilized by radiation.

LONGEVITY AND FIELD ACTIVITY OF STERILIZED INSECTS

The effect of sterilizing dosages of radiation or chemicals on the longevity and field activity of the sterilized insects varies from species to species, depending on the relative susceptibility of each. It must be assumed that most species will show some adverse effects from sterilization, but perhaps not enough to prevent successful control with the sterilization technique. In house flies, for example, continuous feeding on chemosterilants shortens the life-span, but mortality does not begin until after the tenth day, by which time the males have completed most of their normal sexual activity. In many species the field activity of sterilized insects appears to be similar to that of unsterilized insects of the same strain, but colonized insects, which have been used in most sterilization studies, do not always behave like wild strains. Excessively high dosages of radiation, which are required to sterilize some species, may cause the insects to become lethargic, particularly with regard to feeding behavior.

MATING BETWEEN COLONIZED AND WILD STRAINS

Colonized strains of some species of insects are abnormal in behavior, because the colonization process selects for individuals with characteristics for mating, feeding, and ovipositing in confined spaces under abnormal environmental conditions. Before a strain is used in release experiments, studies should be made on the ability of the strain to survive in the natural environment and to compete with wild males for the wild females. Ready mating in the laboratory between colonized males and wild females, or vice versa, does not necessarily indicate that in the field the number of matings between colonized and wild strains will be proportional to the numbers of each that are present in the area. In fact, in the experiments conducted to date, it is doubtful that any colonized, sterilized, and released insects have had the full impact on the fertility of the natural population that would be expected from the ration of their numbers to those of the wild population. However, colonization, with its attendant conservation of space, is essential to mass rearing, and some competitiveness can be sacrificed to obtain the overwhelming numbers needed for release.

CYTOLOGICAL EFFECTS IN REPRODUCTIVE ORGANS

RADIATION

It is well known that ionizing radiation produces cytological abnormalities in the reproductive cells of both male and female insects. These changes range in severity from visible mutations, lethal mutations, mitotic inhibition, and chromosome stickiness to gross chromosome aberrations (chromosome fragments, exchanges, or translocations). There is a definite relation between these cytological effects and insect sterility, but the relation is not always clear. Sterility in males characterized by dominant lethal mutations in the sperm can be attributed to chromosome aberrations, but these cannot be observed in the sperm directly. However, when the sperm from males given a sterilizing dose are used to fertilize an egg, the examination of the egg (or developing embryo) usually shows a variety of gross chromosome aberrations, cytological abnormalities, and mitotic inhibition. Similar cytological changes can be produced in insect oöcytes.

CHEMOSTERILANTS

Antimetabolites

A limited number of antimetabolities, such as aminopterin and amethopterin, are effective as female sterilants, but none has been effective as a male sterilant. Sterility induced in the females by these agents is generally caused by infecundity (failure to produce eggs), but it is not known whether this effect is a result of cytological damage. It is probably related to failure of some process essential to egg formation, but it is possible that these agents could produce cytological damage affecting egg formation, such as in the nurse-cell chromosomes of insect ovaries.

Alkylating Agents

The majority of the effective chemosterilants, such as apholate, tepa, and metepa, are alkylating agents. In general, these chemicals are radiomimetic and produce cytological effects in the reproductive cells of male and female insects. It is well known that alkylating agents (or the products of their biological degradation) affect genetic material. Many of these agents are mutagens, and some produce chromosome aberrations similar to those induced by radiation. In fact, chromosome aberrations have been observed in young embryos derived from untreated eggs fertilized by sperm from a male treated with chemosterilants. It is not known whether this effect will characterize all alkylating agents.

Other Chemosterilants

Except for the antimetabolites and alkylating agents, there are only a few known compounds that are effective chemosterilants. Some of these, such as hempa and hemel, are analogues of alkylating agents. At least one of these compounds is mutagenic, but it is not known whether either or both cause gross cytological effects in the reproductive cells. Eventually, other effective chemosterilants will be developed, and their cytological effects will have to be assessed. However, it is difficult to conceive that any agent that produces male sterility characterized by dominant lethal mutations does not affect the genetic material or produce cytological effects. Chemicals that produce sperm inactivation could have a quite different mode of action. Perhaps some will be found that are nonmutagenic and do not produce cytological damage.

FIELD EVALUATION OF METHOD

METHODS FOR ASSESSING NUMBERS OF INSECTS PER UNIT OF AREA

Most methods of measuring insect populations provide comparisons of relative abundance from field to field or from year to year but do not provide estimates of the total number of insects per square mile or per acre. Estimates of actual numbers present are needed in release programs, to determine the number of sterile insects that must be released per unit of area in order to provide the desired ratio of sterile to normal individuals. Satisfactory evaluation methods are available for only a few species, and the development of such methods is one of the most important areas of needed research. Total counts can be made if the insect is scarce, relatively immobile, and restricted to specific hosts that can be examined readily, as in the northern cattle grub, *Hypoderma bovis* (Linnaeus). Since only the larval stage would be counted, losses in the pupal stage must be known to calculate the number of adults expected in the following generation. Samples taken with sweep nets, emergence cages, traps, or from soil and water, can be used to calculate total populations in a given area only if the infestation rate is uniform and the extent of the infested area is known. Marking, release, and recapture can be used to estimate populations if the released insects can be expected to disperse similarly to the natural populations:

$$\text{Population (including released)} = \text{total trapped} \times \frac{\text{marked released}}{\text{marked recovered}}.$$

EVALUATION OF LIBERATION OF MASS-REARED AND STERILIZED INSECTS

Valuable information on the effectiveness of releasing sterile insects can be obtained in large outdoor cages covering the natural habitat, if behavior and survival are normal. However, the ideal test site is an island sufficiently isolated to prevent natural movement from infested areas. If there is danger of importing the pest through commerce, an effective quarantine must be imposed. Although an oasis in a desert may provide a favorable test site, unexpected rainfall may permit movement of the target species into the test area. Limited isolation can be obtained on a peninsula where most of the test area would be surrounded by water. The importance of isolation is well documented in the eradication of the screw-worm. Based on information obtained during the current eradication program in the southwestern United States, the screw-worm is capable of flying 200 miles or more when conditions are favorable. An attempt to demonstrate eradication under these conditions would require treatment of 40,000 square miles or more instead of only the 170 square miles treated on the island of Curaçao, where it was proved that the sterilization technique could be used successfully to eradicate the screw-worm from an area.

TECHNIQUES FOR RELEASE

Light aircraft are readily modified to distribute sterile insects economically. Since the packaged insects are light in weight, much of the fuselage normally unavailable for cargo can be utilized. A carton dispenser can be timed to yield the desired release rate. The dispenser must be designed to avoid crushing the insects against the fuselage or other structures during release. Fragile insects must be protected from the air blast as they leave the dispenser. This can be done with adequate baffles or by retaining the insects in the carton until it is floating freely. Air conditioners attached to the aircraft are necessary to prevent overheating of the insects when they are being loaded during periods of high temperature. Air scoops near the front of the plane for incoming air and ventilators to the rear will aid in ventilation during flight. Air spaces among the cartons should be provided to insure adequate ventilation.

Ground release of sterile insects is feasible if an adequate road system exists in the treated area. In fact, during weather unfavorable to aircraft operation this may provide the only means for release. However, ground release involves cluttering the roadsides with release cartons, and some insects may be lost to oncoming traffic. In addition, the insects are more concentrated than when released aerially, predation may be increased, and large numbers of insects in a limited area may exhaust their natural food resources.

Attempts have been made to release screw-worms aerially in the pupal stage. However, concussion from striking the ground and predation from ants, birds, and other ground-inhabiting animals may take a heavy toll. Placement of pupae in ground-release containers may result in heavy losses, because various predators tend to congregate near the release site to prey on the inactive, newly emerged insects.

Releases should be timed to avoid extremes in temperature during release. Insects exposed to a hot sun in barren areas may never survive to find food, water, and shelter. During cool periods, the insects would be easy prey to predators active at a lower temperature threshold than that of the released insects. Since food reserves in the newly emerged insect will be depleted with time, releases during warm weather should be made as soon as the insects are capable of flight. However, during cool weather, when food reserves are less critical, it may be advisable not to release insects until they are sexually mature. This would be particularly important in previously untreated areas to assure prompt competitiveness with the natural population. If the treated area is sufficiently large and variable, releases can be shifted to parts most favorable for survival.

Under ideal conditions of uniform insect development, aircraft availability, and environmental conditions suitable for survival, provision of food in the release cartons may not be required. However, under less favorable conditions, provision of food is inexpensive insurance for optimum survival. If release is delayed, survival can be further improved by chilling the insects below the threshold for activity.

The distance required between release lines is dependent on mobility of the released insects and greatly influences the cost of dispersal. The optimum distance may be determined by flying lines considerable distances apart. Fertility checks at various distances from the release lines will show a gradient and determine the minimum distance required between flight lines to obtain uniform coverage.

Although a uniform grid may be desirable in areas where natural populations are fairly uniform, information from ground surveys will allow adjustment of release rates for maximum utilization of the insects. In nonuniform or low-population areas, releases may be restricted to areas of known populations or to known favorable habitats, such as along stream banks or in areas with specific types of vegetation.

EVALUATION OF TREATMENT OF NATURAL POPULATIONS

Sterilization of natural populations may be feasible with safe, effective chemosterilants combined with an attractant. Isolation of the test sites is as important as in experiments with released insects. The baits or other treatments must be distributed so strategically that the exposure of the entire population will be uniform over the entire experimental area.

MEASUREMENTS OF EFFICIENCY

Measurements of the efficiency of field tests should include determinations of the percentage of the natural population sterilized, as well as measurements of the decrease (or increase) in the abundance of the species. Without such information it becomes impossible to assess the factors contributing to the success or failure of the experiment. In tests with released insects, it is also necessary to record their longevity and persistence in the release area.

Sterile insects can be marked with small droplets of lacquer, calco oil dyes, vital stains, fluorescent powders, or radioisotopes. Some mass-reared insects can be distinguished with some degree of accuracy from wild insects by differences in size, conformation, color, or other characters. A genetic marker eliminates the necessity for mechanical marking; however, most mutants may be less vigorous and competitive than the wild strains. Sterile insects can sometimes be distinguished from fertile insects by cytological or gross examination of ovaries and testes. However, this method may be less practical than others because of the time involved and the need for fresh specimens. Sampling the mixed population of released and native insects would give a direct reading of the relative abundance of each. As successive generations of native insects develop, the ratio between sterile and native insects should increase if the sterile insects are effective in reducing the native populations. If conditions for adult survival are unfavorable, both released and native populations should decline. However, the natural population may decline because of unfavorable conditions for immature stages, giving a false impression of the effectiveness of the sterile releases. Collection of eggs from favored hosts to determine hatch may represent the best index of effectiveness; however, collection from insects that oviposit singly or imbed their eggs in the host, or both, would be difficult. Collection of host fruits or plants to determine larval yields may be useful in estimating egg sterility if punctures in the host material are a reliable index of oviposition and correction can be made for other factors affecting larval development. If larval yields are used to indicate natural population density, changes in host abundance must be known.

Even though egg sterility may be high, a normally increasing population may overcome the effects of the sterile-insect release. Conversely, sterility of less than 50% may greatly accelerate a natural decline of the population.

EFFECT OF POPULATION SELECTION WITH CHEMOSTERILANTS

From the time of the first studies with chemosterilants as practical control agents, attention has been given to the possibility that insects could develop resistance to them. Laboratory selection has resulted in the development of resistance to apholate and metepa in the yellow fever mosquito and possibly to apholate in the house fly. However, it was apparent that low dosages of chemosterilants that produced less than complete sterility were nevertheless causing some genetic damage, and that this damage might accumulate from generation to generation. Several colonies of house flies exposed to low dosages of metepa and apholate have exhibited this effect, losing fertility slowly from generation to generation, until the strains died out after a few generations of exposure to treatments that never caused complete sterility in normal flies. In addition, flies reared without exposure to chemosterilants in the laboratory from stock collected on Grand Turk Island, British West Indies, where metepa baits had been used in privies, laid a much higher proportion of sterile eggs than did flies collected on nearby untreated island.

SPECIAL PRECAUTIONS

Insects sterilized by radiation carry no radioactivity and, when released, are no more hazardous to man and beneficial animals than are normal individuals of the same species. However, some types of chemosterilants present special hazards beyond those ordinarily associated with the use of insecticides. Chemosterilants that are alkylating agents are of moderate to high toxicity. All are strongly cumulative in effect. Not only may injury be caused by very small doses of certain alkylating agents, but the injury may take especially undesirable forms, including sterilization, cancer, or teratogenesis. Since developing embryos are especially susceptible to such agents, women of child-bearing age should not engage in research involving the handling of these compounds. Because all known alkylating chemosterilants are absorbed from the skin, and some are also powerful irritants, skin contact, as well as inhalation and ingestion, must be kept to the lowest possible level. In practice this means that work with alkylating agents must be limited to a small number of carefully trained people working under laboratory or factory conditions. Exposure should be minimized by the use of appropriate ventilation, personal hygiene, and, if possible, enclosed systems. Employees working with alkylating agents should have periodic complete blood counts, since an early sign of injury from alkylating agents is a reduction of white blood cells, particularly lymphocytes. Unfortunately, it appears from studies of laboratory animals that the continuing presence of a normal cell count cannot guarantee the absence of serious injury. Fortunately, there is small chance of injury from alkylating agents carried by treated insects, because the amount of chemical they carry is small and the compounds disintegrate rapidly.

Although the analogues of alkylating agents can cause sterility in mammals there is no evidence that they cause teratogenesis, and it is uncertain whether they are weak carcinogens. Of course, they produce systemic toxicity if absorbed in sufficient dosage. Judging from animal experiments, serious injury could probably be prevented if exposure were discontinued as soon as a worker detected irritation or other symptoms. However, until more information is available, the analogues of alkylating agents should be treated with almost as much caution as the alkylating agents themselves.

The antimetabolites that are effective as chemosterilants owe their action to their imperfect chemical and metabolic resemblance to some compound normally present in the body. The toxic effects depend on the vitamin or other properties of the corresponding normal metabolite, and the toxic effect may often be partially counteracted by large doses of the latter. Some antimetabolites, such as aminopterin, are highly toxic, cumulative, and capable of producing teratogenesis. Workers exposed to aminopterin should have repeated complete blood counts. Depending on the compound, it should be possible to devise biochemical tests to predict and thus forestall injury. An example would be measurement of the prothrombin time of persons exposed to antagonists of vitamin K.

INDUCTION OF STERILITY BY RELEASE OF EXOTIC STRAINS

Sterility in insects can also be induced by the suitable manipulation of genetic mechanisms already present in the natural population, including the release of cytoplasmically incompatible strains from other geographical areas. These methods are discussed in Chapter 9.

NEEDED RESEARCH

The use of sterilizing chemicals or radiation offers promise of more efficient control of many pest species than has been possible in the past. The application of these methods to any species, however, requires a thorough knowledge of its population dynamics and sexual behavior not ordinarily available without years of painstaking research. The use of chemicals to sterilize a portion of the natural population depends largely on the development of powerful lures—attractants and stimulants to feeding, mating, and oviposition. Research has followed, and should continue to follow, three principal lines of investigation: a search for safer but more effective chemicals, development of more complete toxicological information on the promising compounds, and development of safe and efficient methods of application based on biological and behavioral studies of each important pest species.

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CHAPTER 16

Insecticides

HISTORY AND PRINCIPLES OF INSECTICIDAL CONTROL

The earliest references to the use of insecticides date back some 3,000 years to the writings of the Greeks, Romans, and Chinese. The toxic nature of arsenicals was known to the Greeks and Chinese during the first century AD, and Homer had recommended the use of "pest-averting" sulfur a thousand years earlier. Despite these early references, the employment of chemicals for the control of insects is largely a development of the nineteenth century. The knowledge of chemical pesticides as recently as a few centuries ago was still based largely on the teachings of Pliny (AD 23-79), which, in turn, drew on the Greek folklore of previous centuries. The slow development in the employment of insecticides was chiefly because of lack of the understanding of the nature of insects. In the absence of specific knowledge, efforts to avert insect attacks were based chiefly on superstition and witchcraft rather than on reason.

The modern use of insecticides in the United States dates from 1867, when Paris green was used to control outbreaks of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). This spectacular success stimulated the imagination of entomologists, and, within a decade, Paris green and kerosene oil emulsion were being employed against a variety of chewing and sucking insects. Meanwhile, the use of Bordeaux mixture as a fungicide with some insecticidal properties was accidentally discovered in France, the discovery adding further impetus to the use of pesticides. In the early part of the twentieth century, fluorine compounds and botanical insecticides were developed. The use of insecticides in the United States had become sufficiently commonplace by the 1920's that concern over residues in foodstuffs began to arise. At this time, regulations were passed establishing tolerances for arsenic and, later, for lead on apples and pears. It was thus recognized that, although insecticides were required, regulation of residues was also needed in the public interest.

The discovery of the insecticidal value of DDT, a synthetic organic compound, in Europe in 1939 was a revolutionary event in the development of insecticides. Its discovery coincided with World War II, and its potential was dramatically highlighted by its wartime uses. Since then thousands of synthetic organic chemicals have been produced, and many have largely replaced the earlier insecticides.

The experiences of the past 25 years have demonstrated the tremendous possibilities for the use of chemicals in insect control as well as the pitfalls resulting from their indiscriminate use. Even now, the commonly used insecticides represent only a few chemical groups, and it seems certain that other groups will be discovered that will provide greater latitude in selection and use. Meanwhile, skill in the formulation and application of available insecticides continues to grow.

The term "insecticide" is derived from the Latin words meaning "insects" and "to kill." A strict interpretation would limit the use of the word to substances that kill and would not include repellents, attractants, chemosterilants, and other chemicals that contribute to insect control in other ways.

Insects are of concern to man because they threaten his food, feed, and fiber; they annoy him and serve as vectors of organisms that produce disease. They also attack his stored goods and his dwellings, creating special problems that often are solved only through exacting research on the most effective means of employing insecticides. There is extensive literature on the specialized employment of insecticides to solve a wide variety of pest problems.

The decision to employ insecticides for the control of insects depends on an over-all assessment of each problem. It must first be determined whether control of any kind is justified. If it is justified, it must be decided what type of control is best adapted to the specific situation. All possibilities, alone or in combination, should be considered, especially one that will fit into an integrated pest-management type of control program. Such an assessment often indicates the need for insecticidal treatments. Experience in handling the complex of insects attacking apples, for example, has shown that an intensive program of insecticidal treatments is required each season to meet the exacting fruit and vegetable market standards that exist in the United States. By contrast, few or no treatments are required for the control of soybean insects.

The guiding principle in such decision-making is that insecticidal treatments are justified only when the expected loss without treatment exceeds the cost of treatment. The application of this principle invokes the need for information on economic thresholds in which pest-population levels and injury are equated. Unfortunately, economic thresholds have been established in very few cases, even for major economic species. Acquiring such information will require economists and entomologists to join in applying sound methods of sampling and in making detailed analysis of production costs. The economic principles of insect control are treated more completely in Chapter 18.

As a starting point in the consideration of insect control by any means, the species must be identified. The rationale in support of this elementary principle is discussed in Chapter 2. When insecticide treatments are deemed necessary, special consideration should be given to (1) effectiveness of the insecticide against the most vulnerable life stage of the pest, (2) employing an insecticide that will cause the least disruption in the ecosystem, and (3) applying the insecticide in a manner that will restrict its distribution to the area where it is needed.

A time-honored principle in the strategy of insecticidal control is that of striking at the pest's "weakest link." This requires exacting knowledge of the insect's identity, life history, and behavior. Control programs are no sounder than the fundamental knowledge on which they are based, and accumulating this knowledge is a challenge to which many entomologists have responded. In seeking to attack a species at its weakest link, a number of variables can be manipulated, such as time and place of attack and the life-history stage against which the control measures are directed. Life-history stages vary in both their susceptibility and vulnerability to insecticide treatment. For instance, the egg stage may be the most susceptible and also the most vulnerable, particularly in a species that overwinters in the egg stage in an exposed position on the host plant. Ironically, even among our best-known economic pest species, we do not have the prerequisite knowledge of their life history and habits to employ control measures with maximum effectiveness. As an illustration, the case of the boll weevil, *Anthonomus grandis* Boheman, might be cited. Despite the years of work devoted to chemical control of this insect, the value of treatments that take advantage of the occurrence of diapause became known only during the last decade.

Insecticides generally are the first line of defense in control of insect outbreaks. They have been employed because: (1) they are highly effective; (2) their effect is immediate; (3) they can rapidly bring large insect populations under control; and (4) they can be employed as needed. Alternative means of control can seldom be found that will provide all these features.

Insecticides, however, are not without limitations; they have very serious limitations, especially in the area of insect resistance to pesticides. Insects become resistant to them. They may disrupt the ecosystem with adverse effects on the insect complex, wildlife, and other desirable species. Residues remaining on treated products may pose health hazards. With an understanding of these problems, it is possible to adjust insecticidal-use practices to maximize benefits and minimize undesirable effects.

The use of insecticides, however, has increased yield, quality, and efficiency of plant production and brought stability to the agricultural enterprise.

The two decades following the general use of synthetic organic insecticides have witnessed a 54% increase in yields. Although this cannot be attributed entirely to insecticides, they are a major factor.

The contribution of insecticides to human health is also impressive. About 30 known diseases are caused by organisms whose arthropod vectors can be greatly reduced or eradicated by insecticide treatments. This list includes such age-old scourges of mankind as malaria, yellow fever, filariasis, bubonic plague, typhus fever, and encephalitis. Malaria, which once accounted for 200 million cases of illness and 2 million deaths annually, has been brought under virtual control on a global scale.

The need and use of insecticides are certain to grow, despite the adverse publicity to which these chemicals have been subjected in recent years. The mechanization of agricultural production to compensate for labor shortages, and the mounting food requirements of an expanding world population, make this necessary. The hope of mankind to escape hunger and disease is closer to reality today than ever before. This hope rests, to a large degree, on continued research and development efforts directed toward the production of safer and more effective insecticides. More efficient use of our present insecticides in well-organized insect-pest management and control programs will greatly increase our worldwide capacity to produce food.

CLASSIFICATION AND CHEMISTRY

Approximately 400 basic insecticides are registered in the United States for the control of pests that damage food, feed, and fiber crops and attack man and animals. Since the middle 1940's the trend has shifted from inorganic and botanical insecticides to the synthetic organic insecticides. It is estimated that less than 10% of the currently used insecticides are inorganic compounds.

Classifications of the major chemical classes of the commonly used insecticides and related chemical control agents follow. Each class includes the following information: type and mode of action, stage or stages in the life cycle of an insect most susceptible to control methods, as well as the name and structure of one or more prominent members of the class. Discussion of any particular group of compounds is rather brief. For a more extensive treatment, pertinent references on systematic listings, classification, and chemistry of insecticides are presented at the end of this chapter.

INORGANIC INSECTICIDES

This once-important class of compounds, inorganic insecticides, includes calcium arsenate, lead arsenate, cryolite, and elemental sulfur. Most of the compounds in this class are toxic to insects primarily by ingestion. One of the better known members in this category is:

Common name: lead arsenate
Chemical name: diplumbic hydrogen arsenate
Chemical structure: $PbHAsO_4$

Arsenic binds the -SH(thiol) groups of enzymes and proteins; therefore, it is considered a general protoplasmic poison for insects. Lead arsenate acts as a stomach poison for the control of chewing-insect larvae and adults. This group of compounds has gradually been replaced by the synthetic organic insecticides because of the following undesirable characteristics: unfavorable mammalian toxicity, persistent residues, the problem of insect resistance, and low efficacy in comparison with synthetic organic insecticides.

ORGANIC INSECTICIDES

Botanicals and Derivatives

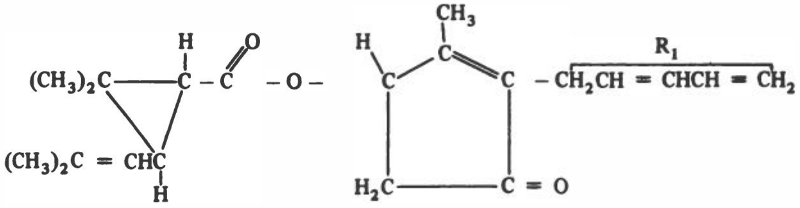
Examples of the botanicals and derivatives are nicotine, pyrethrum, and the derris derivatives (rotenone). These compounds act primarily as contact insecticides. Only pyrethrum is still widely used; it is of value in the control of household, industrial, and stored-food pests. The other compounds in this group have been largely replaced by the newer synthetic organic insecticides.

Pyrethrum is obtained principally from the plant *Chrysanthemum cinerariaefolium* (Visiani). The active toxicants are four esters: pyrethrins I and II and cinerins I and II. These are formed from the alcohols pyrethrolone and cinerolone, and from chrysanthemum monocarboxylic acid and chrysanthemum dicarboxylic acid–monomethyl ester. The cinerins are more stable than the pyrethrins, and pyrethrin I and cinerin I seem to be somewhat more toxic than pyrethrin II and cinerin II. The names and structures of these esters are:

Common name: pyrethrum (composed of four esters)
Empirical formula: Pyrethrin I, $C_{21} H_{28} O_3$
Pyrethrin II, $C_{22} H_{28} O_5$
Cinerin I, $C_{20} H_{28} O_3$
Cinerin II, $C_{21} H_{28} O_5$

Chemical structure:

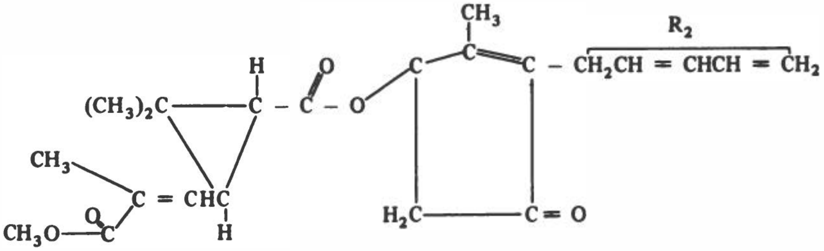
Pyrethrin I:



Cinerin I: has the same structure except

$$R_1 = CH_2CH = CHCH_3$$

Pyrethrin II:



Cinerin II: has the same structure except

$$R_2 = CH_2CH = CHCH_3$$

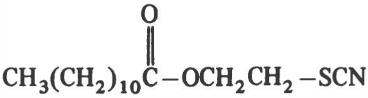
In spite of its high cost and susceptibility to photodecomposition, pyrethrum remains a prominent economic insecticide because of its low oral mammalian toxicity coupled with rapid insecticidal action. This action is potentiated by combination with synergists such as piperonyl butoxide, sulfoxide, *n*-propyl isome, MGK-264 [*N*-(2-ethylhexyl)-5-norbornene-2, 3-dicarboximide], and other synergists that contain the methylene dioxyphenyl moiety. The main toxic principle and exact mode of action of pyrethrum have not been elucidated. Much research is in progress in public and private laboratories to synthesize cheaper, light-stable synthetic pyrethroids.

Organic Thiocyanates

Organic thiocyanates have a rapid paralytic effect that results in good knockdown of flying insects. Thiocyanates are all contact poisons acting on the nervous systems of the insects. Organic thiocyanates are toxic to insect eggs, larvae, and adults. However, their use has been limited by the following: phytotoxicity, dermal irritation, and competition from new synthetic organic insecticides.

Three of the better-known insecticides in this group are Lethane 384 [2-(2-butoxyethoxy)ethyl thiocyanate], Thanite (isobornyl thiocyanatoacetate), and the following:

Trademark: Lethane 60
Chemical name: 2-thiocyanatoethyl laurate
Chemical structure:

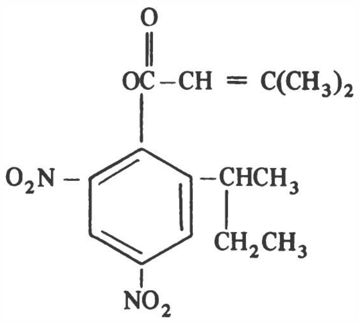


$$\mathrm{CH_3(CH_2)_{10}\overset{\overset{O}{\|}}{C}-OCH_2CH_2-SCN}$$

Dinitrophenols

This classification, dinitrophenols, includes substituted dinitrophenols and their metallic and amine salts. They are effective, by contact or ingestion, against insects and mites in the egg, larval, or adult stage. Poisoning of insects is associated with increased oxygen uptake, enhancement of oxidative metabolism, and interference with production of ATP (adenosine triphosphate). Severe phytotoxicity and some unfavorable pharmacological and toxicological findings have limited the utility of this group of compounds. Binapacryl is a recently introduced contact and stomach acaricide in this group.

Common name: binapacryl
Chemical name: 2-*sec*-butyl-4,6-dinitrophenyl 3-methyl-2-butenoate
Chemical structure:

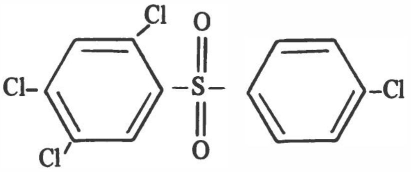


The dinitrophenol moiety is apparently the toxophore in the molecule. Further synthetic manipulations of the molecule may yield additional valuable chemical control agents.

Sulfonates, Sulfides, Sulfones, and Sulfites

A variety of compounds in this classification have been used to a varying degree as contact acaricides. Compounds such as 2-(*p-tert*-butylphenoxy) isopropyl-2′-chloroethyl sulfite (Aramite), 6-methyl-2,3-quinoxalinedithiol cyclic *S*,*S*-dithiocarbonate (Morestan), and *p*-chlorophenyl phenyl sulfone and related sulfones are effective in controlling spider mite eggs, larvae, and adults. Others, such as tetradifon, tetrasul, ovex, and chlorbenside, are effective in controlling only eggs and larvae. Tetradifon has been one of the most successful members of this class. Its designations are:

Common name: tetradifon
Chemical name: *p*-chlorophenyl 2,4,5-trichlorophenyl sulfone
Chemical structure:

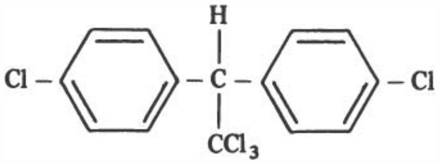


The use of these acaricides has been limited by mite resistance and phytotoxicity problems.

Chlorinated Hydrocarbons

Chlorinated hydrocarbons signaled the development of the synthetic organic insecticides, and they still account for the largest volume of insecticides used each year. They are generally very effective contact and stomach poisons, affecting larvae, nymphs, adults, and sometimes pupae and eggs. They have been of outstanding value in the plant-protection, human-health, and animal-health fields. They are generally less effective in control of piercing and sucking insects, although a number have been used as acaricides. They have no value as plant or animal systemics. In the broadest sense, poisoning in insects is associated with disturbances in the central nervous system that result in hyperactivity, tremors, and incoordination. The best-known insecticide in this class is:

Common name: DDT
Chemical name: 1,1,1-trichloro-2,2-bis(*p*-chlorophenyl) ethane
Chemical structure:



Other well-known members of this class include: benzene hexachloride; lindane; the cyclodienes—aldrin, dieldrin, chlordane, heptachlor, endrin, and toxaphene; and the DDT related analogues—chlorobenzilate, dicofol, and methoxychlor.

The value of this class of compounds has been reduced by highly persistent residues in soils, animals, and plant tissues; accumulation in food chains; nonselectivity to beneficial insects, fish, and wildlife; and insect resistance. In some insect-control situations, these compounds are gradually being replaced by organophosphorus and carbamate insecticides.

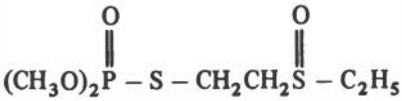
Many of the commercially used commodity and space fumigants are halogenated hydrocarbons. Some of the more commonly used fumigants are methyl bromide, carbon tetrachloride, ethylene dichloride, and ethylene dibromide.

Organophosphorus Esters

The organophosphorus (OP) esters, a growing class of insecticides and acaricides, now numbering some 45 compounds, are the largest and most versatile group of pesticides in use at the present time. They are effective against insects and arachnids by contact, ingestion, or fumigant action. In contrast to the chlorinated hydrocarbons, which have very limited systemic action, the OP esters include several very excellent selective plant systemics, such as dimethyl phosphate, ester with *cis*-3-hydroxy-*N,N*-dimethylcrotonamide (Bidrin), demeton, dimethoate, phorate, and dithiodemeton. These products are absorbed by roots and foliage and are translocated in plants to kill piercing and sucking insects and mites at points distant from the site of application. A plant systemic in wide commercial use is oxydemetonmethyl.

Common name: oxydemetonmethyl
Chemical name: *S*-[2-(ethylsulfinyl)ethyl] *O,O*-dimethyl phosphorothioate

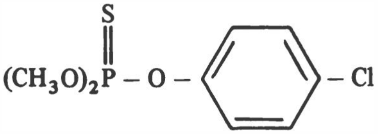
Chemical structure:



$$(CH_3O)_2\overset{O}{\overset{\|}{P}} - S - CH_2CH_2\overset{O}{\overset{\|}{S}} - C_2H_5$$

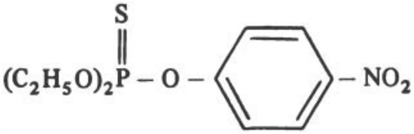
Essentially all stages in the life cycles of insects are susceptible to certain members of this class of compounds. Their versatility is also exemplified by the use of certain compounds as animal systemics to control livestock ectoparasites and endoparasites. Animal systemics must be sufficiently nontoxic to mammals yet highly toxic to insects. Compounds in this category include coumaphos, ronnel, and trichlorfon. One of the most widely used members of this group is:

Common name: ronnel
Chemical name: *O*,*O*-dimethyl *O*-2,4,5-trichlorophenyl phosphorothioate
Chemical structure:



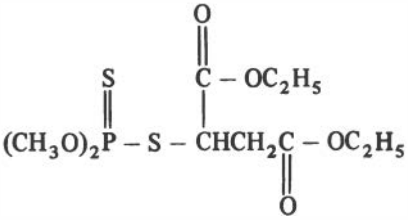
Although the current trend is toward the development of more selective and safer OP insecticides, the most widely used members of this group include one of the most toxic compounds, parathion, and one of the safest to mammals, malathion. Both compounds are illustrated below:

Common name: parathion
Chemical name: *O*,*O*-diethyl *O*-*p*-nitrophenyl phosphorothioate
Chemical structure:



Common name: malathion
Chemical name: diethyl mercaptosuccinate, *S*-ester with *O*,*O*-dimethyl phosphorodithioate

Chemical structure:



$$(CH_3O)_2\overset{\overset{\displaystyle S}{\|}}{P}-S-\overset{\overset{\overset{\displaystyle O}{\|}}{\displaystyle C-OC_2H_5}}{\underset{|}{C}}HCH_2\underset{\underset{\displaystyle O}{\|}}{C}-OC_2H_5$$

Other widely used compounds of this class are azinphosmethyl, carbophenothion, diazinon, ethion, methyl parathion, and trichlorfon.

By analogy to their mode of action in mammals, OP ester insecticides poison insects by irreversibly inhibiting insect cholinesterase(s). Good correlation between intoxication, mortality, and degree of cholinesterase inhibition has been reported for many of the OP insecticides.

Wide acceptance of the OP ester insecticides has been largely because: they can frequently replace persistent insecticides such as the chlorinated hydrocarbons; they act as good substitutes for insecticides that have lost their utility because of insect resistance; they exhibit greater selective toxicity and favorable metabolism; and they are often useful in modern integrated control programs.

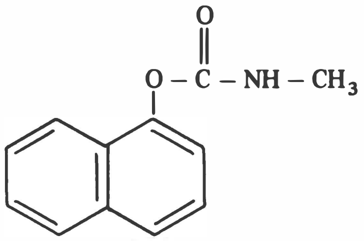
Probably more than 200,000 OP ester insecticides have been synthesized to date, and many more variations of the basic phosphate ester molecule are theoretically feasible. This could result in the development of many additional compounds in this class offering greater selectivity and safety. The number of theoretically feasible molecules in this field is even greater if one considers the many potential phosphonate and, to a lesser degree, phosphinate esters as potential modifications of the basic phosphate molecule.

Carbamates

Compounds in this group are being actively developed as insecticides and, to a more limited extent, as acaricides. A number of heterocyclic carbamates were introduced as insecticides with limited commercial success over 10 years ago. These insecticides included 3-methyl-1-phenyl-5-pyrazolyl dimethylcarbamate (Pyrolan), 1-isopropyl-3-methyl-5-pyrazolyl dimethylcarbamate (Isolan), and dimetilan. Isolan and Pyrolan also showed plant systemic action. However, these compounds had a limited spectrum of activity and high mammalian toxicity and have been replaced by the more recently available OP esters.

The introduction, a few years ago, of carbaryl, a broad-spectrum insecticide, gained renewed recognition for this class of insecticides. The designation of this carbamate is:

Common name: carbaryl
Chemical name: 1-napthyl *N*-methylcarbamate
Chemical structure:



Since the advent of carbaryl, several additional *N*-methyl aromatic carbamate esters have been introduced as contact insecticides effective against insect larvae, nymphs, and adults. Included in this group are 6-chloro-3,4-xylyl methylcarbamate (Banol), *o*-isopropoxyphenyl methylcarbamate (Baygon), 4-(methylthio) 3,5-xylyl methylcarbamate (Mesurol), and 4-dimethylamino-3,5-xylyl methylcarbamate (Zectran).

The mode of action of carbamate esters in insects is analogous to that postulated for the organophosphates, namely, inhibiting the cholinesterase(s) of the nervous system. However, the resulting carbamoyl esterase is apparently less stable than the analogous phosphoryl esterase. According to recent theories, the carbamate ester is hydrolyzed in the process of decarbamylation of cholinesterase. It is thought that cholinesterase inhibition is not the sole poising mechanism responsible for the toxic action of certain carbamates, including the insecticide Zectran.

As with the phosphates, carbamates are readily degraded *in vivo* and in the environment; many have low toxicity to mammals, are selective, and fit well into integrated control programs.

Chemical and biological research is under way to discover more effective and selective aliphatic, aromatic, heterocyclic, and oxime carbamate insecticides. This group, along with the OP esters, offers perhaps the most promising chemical control agents synthesized and developed to date.

Oils

The oils applied to fruit and shade trees are derived from the lubricant fraction of petroleum. They are complex mixtures of hydrocarbons of which the aromatic and other hydrogen-deficient compounds do not exceed 8%. Spray oils are selected on the basis of certain chemical and physical properties, including

(1) distillation temperature at the 50% point and the temperature range between 10 and 90% of the distillation, (2) unsulfonated residue (UR), (3) gravity or density, and (4) viscosity.

Less highly refined oils, called "dormant" oils, were formerly advised for use on deciduous fruit trees during the dormant period. Lighter, more highly refined oils were suggested for use on verdant trees. These were called "summer" oils. The present trend is toward the use of closely similar oils on both citrus and deciduous fruit trees. Some dormant-type oils continue to be used in the western and midwestern areas of the United States, particularly on shade trees. Specifications for oils currently in use to control pests of citrus (in California and Florida) and of deciduous fruit trees (in New York) are listed in Table 5.

Oils of the kinds just defined are effective in controlling mites, especially in the egg stage, and scale insects. Kill is apparently effected by interfering with the gaseous exchange of organisms during respiration. Since deposit must be carefully controlled to avoid plant injury, the oils are usually applied as emulsions and at spray concentrations ranging from 1 to 3%.

The principal limitation of oil use is its potentiality for causing plant injury. This tendency is minimized by using the kinds of oils defined in

TABLE 5 Spray Oil Specifications

Property	New York Superior Oils 60 sec	New York Superior Oils 70 sec	California Narrow Range Oils	Florida Oils FC-435-66	Florida Oils FC-412-66
Distillation at 10 mm Hg, °F (ASTM Method D-1160)					
50% point	408 ± 10	425 ± 12	412 ± 8	435 ± 8	412 ± 8
10–90% range (max)	80	95	65	80	80
Gravity, API (min)	34	33	–	31	33
Percent carbon atoms in paraffinic structure (% Cp) (min) (RI-KVGC Analysis)[a]	–	–	60	–	–
Percent unsulfonated residue (min) (ASTM Method D-483)	92	92	92	92	92
Viscosity (sec) (Saybolt at 100°F)	56–62	66–74	–	–	–

[a] RI-KVGC Analysis is the Refractivity Intercept (RI)–Kinematic Viscosity Gravity Constant (KVGC) correlation, described in the Eng. Exp. Sta. Bull. 152, Ohio State University, 1953

Table 5 and by avoiding their combination with other pesticides with which they are incompatible, such as sulfur, captan, and mercury compounds.

Oils possess two advantages over most pesticides: first, they have been judged to possess such a small human health hazard in use that the Food and Drug Administration of the U.S. Department of Health, Education and Welfare exempts them from a residue tolerance requirement on growing crops; second, pests apparently are incapable of developing races resistant to them. In any event, in the 75 years of oil use, no oil-resistant races have appeared.

Petroleum fractions within the kerosene range are used as carriers or cotoxicants for certain pesticides. However, aromatic petroleum solvents, such as xylene, have become more popular because of their greater solvency properties.

An expanded use of oils in pest control is foreseen. This is expected to come from improvements in oil-refining technology, including the possible introduction of synthetic hydrocarbons, and to meet the pesticide-resistance problems created by failures of competitive products in this regard.

INSECTICIDE DEVELOPMENT RESEARCH

Insecticides, despite their large number and diversity, do not completely fulfill the requirements of agriculture, public health, and the home owner, for safe, efficient, selective, and inexpensive insect control. Demands for new pesticides have arisen as a result of the diversification and mechanization of agriculture and the consequent introduction of new techniques, such as soil fumigation, seed treatments, side-dressings, and the use of plant and animal systemics. Insecticide resistance has been developed by major pests such as flies, mosquitoes, the boll weevil, the codling moth, *Carpocapsa pomonella* (Linnaeus), the cabbage looper, *Trichoplusia ni* (Hübner), the western corn rootworm, *Diabrotica virgifera* LeConte, and phytophagous mites. This situation has produced a steady demand for insecticides with unique modes of action. Increasing awareness of human health and the problems of environmental contamination have resulted in vigorous demands from government agencies for selective insecticides with rapid degradability. In response to these challenges, the chemical industry is developing increasing numbers of new compounds, some produced empirically and many designed specifically for evaluation as to their suitability as insecticides of the future.

DEVELOPMENT OF AN INSECTICIDE

The developmental pathway for a compound showing potentiality as a new insecticide passes through a number of stages of selection of increasing severity and of increasing complexity of evaluation.

TABLE 6 Stages in the Development of a New Insecticide

Stage I	Stage II	Stage III	Stage IV	Stage V	Stage VI
Exploration Testing	Characterization of Performance	Advanced Evaluation Tests	Extended Field Trials	Semicommercial Field Tests	Promotion and Sales
1. Conduct synthesis of new compounds	1. Continue synthesis of related compounds	1. Develop a practical method of synthesis	1. Perfect synthesis methods	1. Conduct large-scale field tests	1. Initiate wide-scale sales activities: Public relations, Advertising, Sales-training schools, Technical service
2. Conduct screening tests for biological activity	2. Make laboratory insecticidal evaluation	2. Conduct small-plot field tests	2. Submit product to experiment stations for field testing	2. Obtain an experimental permit for trial sales if desired	
3. Conduct insecticidal screening tests	3. Conduct range-finding toxicity tests, such as acute oral skin, eye, skin absorption, and inhalation if necessary	3. Conduct 30- to 90-day toxicity feeding studies	3. Initiate long-term toxicity feeding studies on rats and dogs, and if necessary a 3-generation reproductive study	3. Construct production plant	
	4. Improve screening formulations	4. Initiate metabolism studies if required	4. Perfect residue-analysis methods and initiate residue determinations	4. Complete market-potential survey	
	5. Initiate compatibility studies	5. Develop analytical procedures	5. Conduct stability, corrosion, and packaging studies	5. Apply for federal and state label registrations	
	6. File for patent coverage	6. Determine stability of formulations	6. Determine effects on wildlife		
		7. Make preliminary market analysis	7. Construct pilot production plant		

Stage I: exploration for promising compounds through laboratory testing or screening.

Stage II: characterization of the scope of performance, patentability, economics of development, safety, and selectivity.

Stage III: advanced development of analytical procedures, quality control, chronic dietary toxicity, metabolism studies, and patent-filing.

Stage IV: extended field trials in experiment stations, development of a pilot production plant, market analysis, development of label, extensive residue analysis, formulation studies, and reproductive studies over three generations with vertebrates.

Stage V: large scale commercial field trials and development of manufacturing plant.

Stage VI: promotion and sales.

This developmental process is a lengthy one, generally requiring 6 to 8 years for the completion of the six stages; and the selection process is rigorous—a major firm reports that of 4,200 compounds a year entering Stage I, an average of only 27 reach Stage II, and of these only 2 compounds pass to Stage III. Table 6 provides a comprehensive picture of this process.

SCREENING PROGRAMS

The proper evaluation of candidate insecticides is a challenging operation. The large numbers of new compounds available—several firms are screening from 5,000 to 10,000 new compounds a year—and the small quantities generally provided demand simple and precise screening techniques that can be accomplished with a minimum of labor. The mass screening of insecticides requires year-round laboratory rearing of large numbers of test insects produced under standardized conditions. Typical insect species and evaluation techniques employed in governmental, private, and industrial research laboratories are:

Mosquito larvae—*Culex* spp., *Aedes* spp., and *Anopheles* spp.: addition of compound from concentrated solution in acetone or other suitable solvents to water containing larvae and rejection of compounds inactive at 10 ppm.

House fly, *Musca domestica* Linnaeus (both susceptible and insecticide-resistant strains): topical application of 1-μl drop in acetone; exposure to residues on filter paper, glass, or plywood; and exposure to space sprays or aerosols in a small chamber.

Southern armyworm, *Prodenia eridania* (Cramer): exposure to residues on bean leaves dipped into or sprayed with solution or suspension.

Corn earworm, *Heliothis zea* (Boddie): exposure of larvae to treated kernels of canned corn.

Plum curculio, *Conotrachelus nenuphar* (Herbst): exposure to residue on green apples dipped into or sprayed with a solution or suspension.

Mexican bean beetle, *Epilachna varivestis* Mulsant: exposure to residue on bean leaves dipped into or sprayed with a solution or suspension.

Pea aphid, *Acyrthosiphon pisum* (Harris), or bean aphid, *Aphis fabae* Scopoli: spraying or dipping of infested bean plants.

Two-spotted spider mite, *Tetranychus urticae* (Koch) or other species: spraying or dipping of infested bean plants.

Confused flour beetle, *Tribolium confusum* Jacquelin duVal: exposure to fumigant in glass flask, incorporation of compound in standard whole wheat flour, and exposure to residue on filter paper.

American cockroach, *Periplaneta americana* (Linnaeus) or the German cockroach, *Blattella germanica* (Linnaeus): topical application, confinement to residues on treated filter paper, and spraying in small chamber.

The screening operation must strike an appropriate balance between the number of compounds to be evaluated and the desirability of evaluation against as broad a group of pests as possible. Generally, a compromise is made, in that all compounds are screened in Stage I against mosquito larvae, house flies, aphids, mites, or some other insects, which permits rapid identification of promising candidates and rejection of the ineffective compounds. Those showing a satisfactory level of toxicity are then more thoroughly screened against a wider variety of up to 10 species.

Finally, in Stage II of the laboratory screening, those compounds that compare favorably in activity with commercially available insecticides or that appear to have unusual properties of safety, selectivity, or unique modes of action are given a variety of special tests. These tests may include (1) length of residual effectiveness on plywood or mud surfaces, (2) systemic effectiveness when applied to stem or roots of bean or cotton plants subsequently infested with aphids and mites, and (3) systemic effectiveness against animal parasites when fed to small laboratory animals.

FORMULATION

Promising new insecticides from Stage II through the field trials of Stage V involve formulated products suitable for application as dusts or sprays. The ultimate performance of the new product depends largely on the development of formulations that are stable in storage, wet and suspend well, and are convenient and pleasant to handle.

Dust formulations involve intimately mixing the toxicant, generally at 1 to 10%, with a carrier such as talc, pyrophyllite, bentonite, or clay having the proper pH, moisture content, particle size, abrasiveness, absorbability, specific gravity, wettability (where the same product may be used as a water dispersion), and cost. The mixing of toxicant and diluent is carried out by a variety of operations, such as hammer-milling, ribbon-mixing, solvent impregnation, fusing and grinding, and air reduction.

Wettable powders are the most widely used agricultural formulations; they consist of 15 to 95% of the toxicant together with an absorptive carrier, usually a clay such as attapulgite. To promote wetting and spreading, 1 to 2% of surface-active agent is usually added.

Emulsifiable concentrates consist of the toxicant dissolved at 15 to 20 or even 90% in a solvent such as xylene or higher boiling aromatic, kerosene, methyl isobutyl ketone, or amyl acetate, plus the addition of a small percentage of surface-active agent. Important factors determining the choice of solvent are solvency, toxicity to plants and animals, flammability, chemical compatibility, odor, and cost. The emulsifiable product must be balanced to form an emulsion of the proper stability in a wide variety of natural waters with a minimum of agitation.

Other special formulations, such as oil solutions for cattle and household sprays, and granular products for soil treatment and mosquito control, will also be necessary for the wide-scale evaluation of the new product. Considerable interest is being shown in granular over dust formulations, from which they differ only in larger particle sizes. Granules ranging from 30 to 60 mesh have an advantage over dusts in that their greater particle weight minimizes drift, prevents undue loss of insecticide, and reduces contamination of areas bordering those being treated. All these points merit consideration in planning an integrated pest-control program.

Stability in storage is most important for organic insecticides, which are often highly reactive compounds. The solvent or carrier must be chosen to minimize any chance of chemical reaction or heavy metal catalysis. Accessory stabilizers, such as acid inhibitors, antioxidants, and chelating agents, may be necessary to promote stability, and specially lined or treated containers are often essential. Accelerated storage tests at high temperatures must be made to determine the appropriate shelf life of the new product. Phytotoxicity of emulsifiable preparations is a crucial factor in the agricultural use of any new insecticide. A large range of tests on a wide variety of crops under differing climatic conditions is essential before the product is placed in large-scale Stage IV evaluation.

FIELD EVALUATION

The selection through laboratory screening of a compound toxic to one or more species of insects is only the beginning in the development of a new insecticide. Field-evaluation plots with typical emulsions, wettable powders, dusts, and granules under conditions that simulate actual usage are necessary to demonstrate the performance of the new material as compared with standard insecticides already recommended for pest control. Initially, trials are made on small plots consisting of a few rows of crop, 0.01 to 0.1 acre, or on a few fruit trees that have natural insect-pest populations or have been artificially infested with pests reared or collected elsewhere. The plants are sprayed, dusted, or otherwise treated to simulate the actual commercial pest-control practice. The effects on the insect-pest populations are then carefully observed. In the public health field, comparable initial exploratory tests are made by treating 0.01- to 0.1-acre plots for mosquito larvae, or a small hut or barn for observation of the residual activity against adult mosquitoes or flies. These preliminary field tests, which may require 100 to 500 g of technical compound, afford a valuable opportunity to observe objectionable properties of the compound, such as phytotoxicity; instability to light, air, and moisture; toxicological manifestations, such as skin irritation, photosensitization, violent cholinergic properties; or lachrymatory and sternutatory effects. The appearance of any of these will markedly affect the course of subsequent investigations.

If the compound performs satisfactorily in these tests and other data are uniformly favorable, the screening process enters Stage IV—extended field trials. Early in this stage the commercial developer determines that the compound has a likely future and decides to invest some $500 thousand to $1 million in its development. A small pilot-plant operation produces about 50 to 2,000 lb of technical material which is formulated and blended into standard formulations. These are furnished in small lots, e.g., 50 to 100 lb of wettable powder and 5 to 10 gal of emulsifiable formulation, to federal and state experiment stations located in areas where the experimental material is believed to have potential value in crop protection.

In Stage IV it is essential to measure the persisting residues on agricultural commodities resulting from normal field use. Such information is essential in the application for the establishment of residue tolerances and is normally carried out on a variety of crops and under widely differing climatic conditions, through the cooperation of state and federal experiment stations. It is essential to have analytical data of great sensitivity, with specificity for both the insecticide and its important metabolites, when determining the rate of disappearance of a residue and the final residues, after harvest from recommended treatment schedules of multiple applications of sprays, either dilute or concentrate, on the crops and animals where the compound will be used.

International agencies such as the World Health Organization and the Food and Agriculture Organization of the United Nations set international standards for pesticides and their safe usage, maintain panels and discuss important problems in pesticide development, and carry out screening operations and field development programs for new pesticides. Through their efforts, it is possible to evaluate a new insecticide on a global basis against an enormous variety of pests and under nearly every condition of usage.

DEVELOPMENT OF ANALYTICAL METHODS

Early in Stage III it is essential to develop analytical procedures for the precise quantitative determination of the active ingredient in technical and formulated products and for the microestimation of residues of (1) the active ingredient; (2) its oxidative, hydrolytic, or photochemically formed derivatives present in or on various surfaces, such as those of plants and walls; and (3) metabolic derivatives of the active ingredient formed by biochemical reactions in the tissues of treated plants or animals.

Suitable analytical methods for residue analysis should have a sensitivity in the range of 0.001 to 0.01 ppm and should be able to support or confirm the identity of the insecticide and its specific degradation products. The following types of measurements have been successfully adapted to the analysis of insecticide residues.

1. Chemical measurement: color formation or blanching; gas generation or absorption; pH changes; precipitation; and emission of radioactivity.
2. Physical measurement: chromatographic separation by adsorbent on column or thin layer on paper, by ion exchange, gas chromatography, or electrophoresis; polarography; spectrophotometry by ultraviolet, visible, infrared, fluorescent, nuclear magnetic resonance, gamma ray from neutron activation, mass, or x ray; and amperimetric or potentiometric titration.
3. Biochemical measurement of the quantitative inhibition of an enzyme such as cholinesterase by insecticides, as, for example, by OP compounds and carbamates.
4. Bioassay: using the precisely determined dosage versus mortality curve with living organisms such as mosquito larvae, the adults of *Drosophila* spp. and the house fly, and mixed ages of *Daphnia* spp.

The most popular general analytical methods are colorimetry, infrared spectrophotometry, gas chromatography, and enzyme inhibition. These all lend themselves to relatively simple analytical procedures and generally permit the ready isolation (cleanup) of the microcontaminant from the large volume of interfering substances present in plant and animal tissues.

METABOLISM STUDIES

Increasing concern about long-range chronic effects resulting from exposure of man and other animals to pesticides and interest in the development of biodegradable pesticides are responsible for the necessity for detailed metabolic studies of the fate of a new candidate insecticide in plant and animal tissues. Such metabolic investigations are usually carried out by using isotopically labeled molecules containing ^{14}C, ^{3}H, ^{35}S, ^{36}Cl, or ^{32}P. The labeled compounds are isolated from tissued breis by column, thin-layer, and paper chromatography. The labeled fragments of the parent insecticide are identified by microchemical reactions, comparison with synthetic derivatives by isolation, and spectrophotometric investigation. Metabolism studies are aimed at producing a complete metabolism scheme and balance sheet for the ultimate degradation of the compound to simple moieties such as CO_2, to compounds stored in fatty tissues, and to water-soluble derivatives that may be excreted in animal urine.

These investigations provide basic information, not only for safety when using the insecticide, but also for the development of analytical methods for residues in plant and animal tissues, particularly with compounds such as the systemic insecticides. Some of the compounds may undergo substantial transformations to more or less toxic metabolites. In the search for new animal systemics and parasiticides, radiotracers of all promising compounds are administered to test animals. Any that are not promptly and totally excreted are discarded.

ANIMAL TOXICOLOGY

Animal toxicology plays a dominant role in determining the development and usage of a potential insecticide. The results of preliminary Stage II studies of the acute oral and dermal LD_{50}, which consist of 30-day feedings, and 8-hour inhalation of saturated vapors to rats, guinea pigs, or rabbits, determine the safety of the compound in manufacturing processes and in its general distribution to persons in agricultural or public health operations, and dictate precautions for handling. If the compound progresses to Stage III, it is fed to rats and dogs for 90 days, with comprehensive studies of weight gain, blood pathology, and liver- and kidney-function tests. If it is decided to register and market the compound, longer term chronic studies are initiated in Stages III and IV, involving feeding for 3 generations in rats and mice and

2 years in rats and dogs, and fertility studies are made in Japanese quail, *Coturnix coturnix japonica* Temminck and Schlegel. Knowledge of the metabolism in plants and animals is needed so that the important metabolites can be synthesized and their acute and subacute toxicities established. Because of the lengthy period required for the developmental process, it is most important to initiate and plan the long-term toxicity studies for a compound as early as possible.

When a residue of the insecticide (or any of its degradation products) is likely to be present in or on food crops or animals, it is necessary to request the Food and Drug Administration, Department of Health, Education and Welfare, to establish a tolerance for the residue in the crops or animals involved. A petition for a tolerance includes the toxicity data described above, as well as data to show the amount of residue likely to be present in the food. The tolerance-setting procedure ensures a high degree of safety for the ingestion of such residues in food. Usually a safety factor of at least 100-fold must exist between the lowest "no-effect" level observed in laboratory animals and the amount likely to be ingested by humans. Compounds that have been judged by tests appropriate for the evaluation of the safety of food additives may not have had tolerances established as to their quality to induce cancer in man or animals.

The final portions of the toxicological evaluation come in Stages IV and V, where large-scale usage gives an opportunity to detect allergenic reactions, photosensitization, and other effects.

ECONOMICS OF RESEARCH AND DEVELOPMENT

The total cost of pesticide development is difficult to assess. Various commercial companies have cited figures ranging from $500 thousand to $4 million. The detailed analytical, metabolic, and toxicological studies are costly, and the higher figure is probably representative for a broad-spectrum insecticide such as malathion or carbaryl. The total cost would be substantially higher if the figures included the cooperative services of state and federal experiment stations, which may extend over several years in Stages IV and V.

This extremely expensive development would not normally be risked were it not for the exclusive protection granted the commercial developer under United States patent policy. For this reason, emphasis is on new compound research and on new compositions of matter where patent protection can be obtained.

TOXICITY AND FATE OF INSECTICIDES

MODE OF ACTION

Originally, the classification of insecticides was based on their toxicity to the insect as determined by mode of entry; for example, stomach insecticides, e.g., lead arsenate, are toxic when ingested; fumigants, e.g., hydrogen cyanide, enter as a gas through the spiracles; and contact insecticides, e.g., nicotine, penetrate the cuticle. More recently, an additional group appeared, comprising residual insecticides, such as DDT, which enter through the pulvilli on the tarsi when the insect contacts a sprayed surface. It is now evident that many insecticides can act in several ways. For example, fixed nicotine acts as both a contact and a stomach poison, and lindane, a residual insecticide, in addition to being a contact and stomach poison, acts as a vapor toxicant. The true classification should concern the toxicological action of the insecticide on the vital tissues and enzyme systems.

The older insecticides were general poisons and merit the name of biocides. For example, arsenicals, such as Paris green and lead arsenate, attack the gastrointestinal epithelium in insects as in higher animals, combining with the SH^- groups of the cellular metabolism of insects and mammals by inhibiting cytochrome oxidase as well as other metal-containing enzymes, such as phenoloxidase and catalase.

The next insecticides to appear were less general and more specific to insects. The dinitro compounds, such as 4,6-dinitro-*o*-cresol, kill insects by uncoupling the system that normally transfers the energy from the oxidation of ketoglutarate and many other substrates into the phosphorylation of adenosine diphosphate to produce adenosine triphosphate. They quickly penetrate the cuticle to paralyze the muscles of insects. Man is protected to some extent, but not completely, against dermal doses of dinitro compounds.

Rotenone, a botanical insecticide, paralyzes insects by inhibiting the reoxidation of nicotinamide-adenine dinucleotide. It is also a fish poison but normally presents little hazard to mammals, except to hogs.

Some of the newer synthetic organic chemicals, e.g., malathion and carbaryl, are true insecticides rather than general poisons in that there is a vast difference between their potency against insects and their small or nonexistent hazard to higher terrestrial animals. They are usually nerve poisons, and there are several possible reasons why they have a differential toxicity to insects as compared with higher terrestrial animals. The nerves of insects are more accessible to the insecticide than are the nerves of mammals. There are also differences in the metabolism of insecticides by insects as contrasted with higher animals. Even among vertebrates, species differ in their ability to oxidize phosphorothionates and phosphorodithioates (and thus produce a toxic molecule). Azinphosmethyl has approximately equal toxic effects on rats and insects; both kinds of animals readily oxidize this compound. The phosphinodithioic analogue of azinphosmethyl is differentially toxic to insects and rats; insects readily oxidize this compound but rats do not.

A theory has been proposed that the fundamental effect of DDT on insect nerves is to impede the requisite instantaneous movements of potassium ions through the neuron membrane; thus, the nerve fails to repolarize immediately after the action potential has passed; instead, the poisoned nerves enter a condition of repetitive discharge that throws the muscles into tremors (the DDT jitters) and finally locks them in a tetanic paralysis. In practice, the DDT deposits first affect the sensory nerve endings at the cuticular sensillae, and the repetitive discharge is carried through the reflex arc of ganglia and motor neurons. When an insect is poisoned with DDT, the nerves liberate into the hemolymph one or more neurotoxins (probably aromatic amines) that upset the system. Neurotoxins are produced continuously in response to the nerve-unstabilizing action of DDT. They are unstable by themselves and have only a transitory effect on nerves, from which the nerves can completely recover. If they are produced over a prolonged period of time, they may cause a permanent effect on the nervous system, in that phosphorylation becomes uncoupled and eventually cellular derangement becomes visible in the nucleus and cytoplasm. DDT has the same initial effect as the pyrethrins, which act on the nerve axons and induce repetitive discharges. However, the more rapid knockdown effect of the pyrethrins is balanced by their liability to be detoxified so that the insect can recover, which seldom happens with DDT.

The fundamental mode of action of the cyclodiene derivatives is unknown. Many of them are epoxidized to more active toxins, e.g., aldrin to dieldrin and heptachlor to heptachlor epoxide, but chlordane cannot be epoxidized. The balance of evidence is that these derivatives affect the ganglia rather than the axons, and so their action is central rather than peripheral. Normal action potentials passing through dieldrin-poisoned ganglia emerge as repetitive discharges in the motor nerves. Later, the Nissl granules in the neuron cell bodies fade away, while the nuclei in the forebrain become denser. Gamma benzene hexachloride, or lindane, is also a ganglionic poison, acting faster than the cyclodiene derivatives because it can enter through the spiracles. The original type of ganglionic poison is nicotine, which, for unknown reasons, initially facilitates the conduction of impulses across the synapses but finally blocks them entirely.

The OP compounds, which are now available in great variety, are also ganglionic poisons, causing facilitation and blockage at the synapses. They are oxidized in the insect, e.g., malathion to its oxygen analogue, to the active toxicant that inhibits the enzyme cholinesterase needed to destroy the neurotransmitter acetylcholine whenever it is liberated at the synapses as the action current crosses it. The accumulation of acetylcholine first causes facilitation, and the insect becomes hyperactive while its internal glands pour fluid into the alimentary canal. It then causes blockage, so that the legs are extended in paralysis and the insect dies with a considerable proportion of its cholinesterase inhibited.

The most recent group, the carbamate insecticides, also act by inhibiting cholinesterase, and, in this instance, they resemble the natural substrate acetylcholine. They have a marked muscarinic effect, rather like nicotine, and the insect develops tetanic spasms before the paralysis. However, since the carbamate insecticides, e.g., propoxur, carbaryl, and dimetilan, inhibit the cholinesterase by carbamylation rather than phosphorylation, the inhibition is more readily reversed than with OP poisoning.

SPECIFICITY

Most insects are not injurious, and, ideally, an insecticide that affects only the target species should be employed. Unfortunately, such a high degree of selectivity has not yet been achieved. Although many insecticides are effective against a broad spectrum of insect types, a particular pest species is often more effectively controlled with certain insecticides than with others. Some exceptions to this are the systemic insecticides, which may be incorporated in the soil. The systemics are then absorbed by the roots of the plant and translocated to the aerial parts of the host. Thus, only injurious insects that suck juice from the treated plant or devour its tissues are directly affected by the toxicants, except when these insects may be consumed by predators.

Whatever specificity a given insecticide possesses usually derives from its relative ease of entry into the insect and to the active sites of poisoning. Nicotine was a specific for aphids because it was a potent contact insecticide and readily penetrated the nervous system, while Paris green was the choice material for the Colorado potato beetle because it was a suitable stomach poison. DDT is particularly effective against house flies and adult mosquitoes because it is a residual insecticide, and against mosquito larvae and caterpillars because its toxicity is caused by contact as well as stomach action. Many beetles, however, that have heavy cuticular defenses, require the cyclodiene derivatives as chemical control agents on nonedible crops, e.g., the boll weevil on cotton. Soil-inhabiting beetle larvae, such as wireworms, rootworms, and white grubs, are also combated with aldrin, dieldrin, or heptachlor when worked into the ground, but the long residual presence of these compounds is restricting their use.

Specificity may also occur because some insects can detoxify a given insecticide and others cannot. The normal species characteristics of the house fly and the tomato hornworm, *Manduca quinquemaculata* (Haworth), are such that they cannot detoxify DDT, but the tobacco hornworm, *Manduca sexta* (Johannson), grasshoppers of the genus *Melanoplus*, the western bloodsucking conenose, *Triatoma protracta* (Uhler), and the Mexican bean beetle can detoxify DDT and thus are naturally somewhat tolerant of this insecticide. The red-banded leaf roller, *Argyrotaenia velutinana* (Walker), resembles grasshoppers in absorbing very little DDT and immediately detoxifying the amount absorbed. The light brown apple moth, *Austrotortrix postivittana* (Walker), of Australasia is another species of tortricid that is controlled much better by TDE than by DDT. The botanicals, pyrethroids and rotenoids, are also exceptional insecticides in that they are quite toxic to nearly all insects.

In seeking toxicological specificity, we are forced to recognize that biochemical systems of animals have much in common; thus, it is difficult to provide complete specificity, which would protect beneficial insects, man, and wild and domestic animals. However, differences do exist that can be exploited in developing selective insecticides. The tailoring of selective or narrow-spectrum insecticides has been handicapped by factors involving toxicological and economic principles. Our knowledge of mode of action and the relationship of molecular structure to toxicity has been too limited to provide a basis for "blueprinting" selective insecticides.

INSECT RESISTANCE TO INSECTICIDES

The term "resistance" is applied to formerly susceptible species of insects, populations of which can no longer be controlled by a given insecticide at the rates normally recommended. The new population tolerates doses that formerly killed almost all its progenitors. The first instance of resistance in the United States was noted in 1908, when the San Jose scale, *Aspidiotus perniciosus* Comstock, resisted lime–sulfur sprays in certain orchards of Washington State. Subsequently, three species of scale insects resisted HCN fumigation in California between 1912 and 1925, and the codling moth became resistant to spray deposits of lead arsenate in Colorado by 1928. A notable example outside of the United States was the first case of resistance to DDT in the house fly, which appeared in Sweden in 1946. Some 224 species of insects and acarines in various parts of the world have developed resistance to one or more groups of insecticides; of these, 127 are agricultural pests and 97 are pests of medical or veterinary importance. Fortunately, developed resistance to DDT apparently does not involve a cross-resistance to cyclodiene derivatives or lindane, and vice versa, and none of these resistances carries a cross-resistance to OP compounds. Of these three resistance types, DDT resistance has appeared in 89 species; cyclodiene or lindane resistance, or both, in 116 species; and OP-resistance in 39 species; there are many populations in which two or three of the resistances are present simultaneously. A few insect species have become resistant to arsenicals, HCN, tartar emetic, selenium, cryolite, rotenone, pyrethrins, and carbaryl. Also, certain of the tetranychid mites have developed resistances to ovex, chlorobenzilate, dicofol, and tetradifon.

Resistance is a character developed by selection within a population of a species normally susceptible to a particular insecticide. It is an inheritable characteristic, developing only in populations that already have the factors for resistance, and not inducible by habituation during the lifetime of the insect. Thus, resistance is not postadaptive but is preadaptive, deriving from genetic factors that are, in fact, mutant-type alleles of genes for susceptibility. It can be induced only by differential mortality, the insecticidal treatment acting as the selecting agent to eliminate the bearers of the susceptibility alleles and to favor the genotypes carrying the resistance alleles. In essence, it involves a population of susceptible homozygotes for the resistance alleles.

It has been proved that resistance is caused mainly by allelism for a single gene. Cyclodiene-resistance is so clearly monofactorial that the three genotypes can be clearly distinguished from one another by their respective dosage–mortality regression lines, the hybrid heterozygotes being exactly intermediate and completely distinct from either parental homozygote type. By the use of marker genes, it has been possible to find the precise location of this gene on one of the three chromosomes of the mosquito *Aedes aegypti* (Linnaeus). Similar precision probably will be achieved shortly for the dieldrin-resistance genes in the mosquito *Culex pipiens* (Linnaeus), the house fly, and the German cockroach. As a rule, DDT resistance is the result of a single gene, but the dosage–mortality lines of hybrids and parents usually overlap, and a second genetic factor is often detected. In the pomace or vinegar fly, *Drosophila melanogaster* (Meigen), the main DDT-resistance gene is located on chromosome 2, with an enhancer gene on chromosome 3. In the house fly, the main gene determining kill resistance is on chromosome 2. In *A. aegypti*, the main DDT-resistance gene is located very close to the cyclodiene-resistance gene on chromosome 2; yet in *C. pipiens* these two genes are, respectively, on chromosomes 2 and 3. Organophosphorus resistance usually develops as a polyfactorial system from which one gene finally emerges as the deciding one. The OP-resistance allele is usually dominant and has been located on chromosome 5 in several strains of the house fly. The only resistance gene found to be linked with the sex chromosome is that for HCN resistance in the California red scale, *Aonidiella aurantii* (Maskell); thus, males are haploid for it, as they are for the entire chromosome complement in tetranychid mites.

The physiological mechanisms through which the insect could derive its resistance were fully investigated in the house fly. One single abnormality was decisive, namely the ability of resistant flies to detoxify DDT by breaking it down into HCl and DDE [2,2-bis-(*p*-chlorophenyl)-1,1-dichloroethylene], a nontoxic analogue. The detoxification was achieved by an enzyme called DDT–dehydrochlorinase, protein of 36,000 mol wt. Requiring glutathione as an activator, it could also dehydrochlorinate DDD and methoxychlor, and thus the house flies were cross-resistant to these DDT analogues.

DDT–dehydrochlorinase is produced by the resistance allele on chromosome 5, and the homozygotes develop twice as much of it as do the heterozygotes. DDT resistance in mosquitoes and several other insects is associated with the detoxification to DDE, although the DDT–dehydrochlorinase enzymes in *Aedes* and *Culex* spp. differ in their substrate specificity. However, the DDT–dehydrochlorinase in the body louse, *Pediculus humanus humanus* Linnaeus, working only in resistant lice, although equally present in susceptible ones, produces a mixture of DDA [2,2-bis (*p*-chlorophenyl) acetic acid] and DBP (dichlorobenzophenone). In the pomace fly and the German cockroach, the DDT is not dehydrochlorinated to DDE but is oxidized to dicofol.

Dieldrin is not broken down by resistant to susceptible house flies, although in mosquitoes it is slowly metabolized to aldrin, glycol, and other products. Lindane, however, is dehydrochlorinated and further broken down to a dozen metabolites by the house fly; moreover, resistant strains metabolize more and absorb less than susceptible strains but the differences are too small to account for the resistance. It is significant that lindane placed directly on the ganglia of resistant flies has no effect on the action potentials. It is therefore possible that this ganglionic resistance is the factor that causes cyclodiene resistance and cross resistance to lindane. A higher lipoid content is frequently found in cyclodiene-resistant strains of mosquitoes and sometimes in house flies. However, it is probably a minor vigor-tolerance factor sufficient to cause a difference between individuals of a generally susceptible strain in their response to dieldrin poisoning.

The physiological mechanism of OP resistance has usually proved to be detoxification. The specific resistance to malathion in *Culex tarsalis* (Coquillett) is caused by a greatly increased production, by a single gene allele, of a carboxyesterase enzyme which hydrolyzes the side chain. Resistance to parathion and diazinon in the house fly is brought about by phosphatase-type breakdown enzymes produced at the expense of the normal aliesterase activity. It appears that alleles of the gene on chromosome 5 produce esterases capable of splitting OP compounds instead of being inhibited by them; but another allele at this locus imparts carboxyesterase activity and malathion resistance. In American strains of the two-spotted spider mite, OP resistance is also caused by increased detoxification, but in one European strain it is derived from a less sensitive cholinesterase. The resistance to the carbamate insecticide carbaryl developed in house flies by laboratory selection proved to involve an increase in detoxification by nonspecific esterases. HCN resistance in the California red scale, originally attributed to an abnormal readiness to close the spiracles, was later concluded probably to be because the cellular respiration was of a type that depended less on the cytochrome oxidase system.

Attempts have been made to devise countermeasures for resistance based on the biochemical understanding of the resistance mechanism. For example, inhibitors of the detoxifying enzymes may be added as synergists. DDT–dehydrochlorinase is inhibited by the compounds 4,4′-dichloro-*a*-methylbenzhydrol (Dimite) and *N*,*N*-dibutyl-*p*-chlorobenzenesulfonamide (WARF antiresistant for DDT), and initially they proved to be effective synergists against DDT-resistant house flies and mosquitoes. But, being close relatives of DDT, they are merely competitive inhibitors, so that house flies can eventually develop resistance to the synergist–DDT mixtures by containing more DDT–dehydrochlorinase. This "mixture resistance" appears to develop more slowly with WARF antiresistant than with other analogues. As inhibitors for detoxification, certain synergists are also available for OP insecticides, such as EPN (ethyl *p*-nitrophenyl phenyl phosphonate) as a carboxyesterase inhibitor, tributyl phosphorothioate as an aliesterase inhibitor, and propylparaoxon as a phosphatase inhibitor. The well-known pyrethrin synergists, such as piperonyl butoxide, often have some synergistic effect for OP compounds, carbamates, and even DDT, partly because they inhibit esterases in general.

Certain analogues cannot be detoxified by the resistance-mechanism enzymes. For instance, Dilan, a mixture of Bulan [1,1-bis (*p*–chlorophenyl)-2-nitrobutane] (approximately 2 parts) and Prolan [1,1-bis (*p*–chlorophenyl)-2-nitropropane] (approximately 1 part) cannot be dehydrochlorinated by DDT-resistant house flies, because its constituents lack the chlorine in the aliphatic central chain. The DDT–dehydrochlorinase of *Aedes aegypti* (Linnaeus) cannot detoxify deutero-DDT, and that of *Culex fatigans* (Wiedemann) can do it only slightly. This nonradioactive isotopic analogue is also an effective insecticide against DDT-resistant bollworms, but it can be dehydrochlorinated as readily as DDT by resistant house flies. The carbomethoxy analogue of malathion cannot be detoxified by the carboxyesterase of *Culex tarsalis* (Coquillett). Certain OP compounds, such as ethion and carbophenothion, elicit very little resistance in tetranychid mites.

In practice empirical tests are made to discover substitute insecticides that are effective against the resistant strains. Thus dieldrin and lindane were used as remedial insecticides for DDT resistance, to be followed almost without exception by the development of cyclodiene or lindane resistence. This brought the new OP insecticides into play, but now some species, such as the house fly and *Aedes nigromaculis* (Ludlow), have run the whole gamut to include OP resistance. The situation was reversed with the tetranychid mites, the chlorinated acaricides being introduced as remedial toxicants for OP resistance, with the final outcome a resistance to chlorobenzilate, dicofol, and tetradifon. Insects resistant to either type of chlorinated hydrocarbons have frequently remained susceptible to OP compounds, e.g., root maggots to diazinon, although the OP compounds never give the long residual protection provided by the chlorinated cyclodienes. Even with OP-resistant house flies, there are certain OP compounds (1) that are so potent, e.g., fenthion, that they can achieve control despite the generally decreased OP susceptibility; (2) that may be presented as baits, e.g., trichlorfon, thus assuring a heavy dose per insect; (3) that may continue to give off toxic vapors, e.g., dichlorvos, against *Anopheles* mosquitoes in houses; and (4) to which resistance and cross-resistance fail to develop e.g., dimethoate.

It was hoped that the substitution of an insecticide in a new group would result in the reversion or loss of resistance developed in the original group. But experience with house flies has shown that, even in cases where resistance to chlorinated hydrocarbons has reverted to susceptibility because of the use of OP compounds, the original resistance is rapidly regained when the chlorinated hydrocarbons are reapplied. It was also hoped that resistance could be forestalled by mixtures of two insecticides, one to kill the survivors resistant to the other, or alternations of two different types of insecticides. But prolonged selection experiments on house flies and cockroaches resulted in the mixtures or alternations producing two insecticide resistances in the same period as one. With orchard mites, however, the rotation from the chlorinated hydrocarbons to an OP to an S-containing acaride in successive years has achieved delay in the onset of OP resistance. The development of resistance to one insecticide has occasionally been accompanied by an increased susceptibility to another, but this negative correlation is meaningful only if it involves one and the same gene allele. Such is the case in the increased susceptibility to phenylthiourea imparted by the DDT-resistance allele on chromosome 2 in the pomace fly; thus, DDT and phenylthiourea select in opposite directions, and each corrects the resistance to the other. Unfortunately, this particular negative correlation does not hold good in mosquitoes or the house fly.

In countering the insecticide resistance problem, reliance should be placed not in discoveries or breakthroughs but in the avoidance of errors. Resistance is the result of Darwinian selection and should be expected to develop wherever insects are exposed for long periods to selecting levels of the insecticide that causes some degree of mortality short of 100%. The change toward resistance will be more abrupt when the selecting level in terms of percent mortality is higher, and there will be less delay in its development when the area contaminated with the insecticide is wider and the surrounding untreated population is smaller. Residual insecticides are perfect selecting agents because they persist for such a long period at selecting levels of contamination. The only species that will fail to develop resistance under such conditions are those lacking the appropriate resistance allele in their gene pool or those in which the resistance allele is deleterious to survival. This is the only conceivable reason why the European corn borer, *Ostrinia nubilalis* (Hübner), has not developed DDT resistance and certain populations of *Hylemya cilicrura* (Rondani), a root maggot on tobacco, have been slow to develop the cyclodiene resistance, which now characterizes the parallel populations of *H. liturata* (Meigen). It is therefore always prudent to expect resistance to develop in any arthropod pest treated year after year with residual insecticides and to take appropriate steps to delay its onset and to detect its appearance.

Steps to delay resistance might include the replacement of highly persistent residual insecticides or using them only in restricted areas: (1) in preplant, at planting, in postplant, or side-dressing row treatments, instead of in broadcast whole-field applications; (2) in baits rather than in sprays or dusts; (3) as seed treatments; or (4) in planting water at the time of setting plants. In a wider context, chemical control should be joined by a greater variety of control methods—biological, genetic, and cultural—and be allowed to find its proper place as an element in integrated control (see Chapter 17).

Measures to detect resistance include devising and using standard test methods to assess the current susceptibility levels of the treated populations and to anticipate the control failures which would only serve to stabilize the resistance. Such methods, which make it possible to determine the LD_{50} (or LC_{50} or LT_{50}) of the treated population for comparison with that of an untouched field population or laboratory colony, have now been standardized by the World Health Organization for most of the insects of public health importance. Similar steps toward standardization of test methods for determining resistance in the agricultural field are being taken by the Entomological Society of America.

Resistance continues to be a problem, but it has not been the avalanche that some predicted. Its advance has been steady, like a glacier, affording sufficient time to devise appropriate countermeasures and to learn how to live with it. Although the resistance of certain insects to insecticides has been known for a long time, the importance of this phenomenon gained widespread attention after continuous and intensive use of the highly persistent chlorinated-hydrocarbon insecticides introduced in 1945. The practical outcome has been the substitution of a great variety of OP compounds. Although the end result is regrettable because of the increased cost of control, it is also fortunate in that it accelerates the trend away from chemicals that may accumulate as undesirable residues.

DEGRADATION AND FATE IN THE ENVIRONMENT, PLANTS, AND ANIMALS

The chlorinated hydrocarbons and other residual insecticides were originally developed principally for their stability. DDT is relatively indestructible and is not appreciably volatilized until the air temperature exceeds 40°C. When dissolved in oil or some other organic solvent, DDT is destroyed by ultraviolet light, the photolysis producing DDE and dichlorobenzophenone. It is also slowly dehydrochlorinated in the presence of Fe ions. Dieldrin is almost as nonvolatile as DDT and is stable to light. Lindane, although photostable, is appreciably volatile and is broken down to trichlorobenzenes in alkali or in contact with Fe ions. The residual OP insecticides are less persistent but are appreciably volatile; parathion is hydrolyzed slowly by water to nitrophenol and diethylthiophosphate; malathion is decomposed in mild acid or with iron; and diazinon is slowly hydrolyzed in water and on metal surfaces.

The organic residual insecticides accumulate in soil, but not to the same extent as the more durable inorganic biocides that they replaced. Accumulations of arsenic in a few orchard soils had reached the astounding figure of 1,400 lb/acre (as As_2O_3). Cotton productivity in sandy cotton soils had been adversely affected by the presence of arsenic. Accumulations of DDT in orchard soils now range up to 100 lb/acre, and some cornfields contain as much as 10 lb/acre. The rate of loss of DDT over a 10-year period in soils treated against the Japanese beetle, *Popillia japonica* Newman, proved to be 80% for heavy applications and 90% for light applications.

Ninety percent of aldrin thoroughly mixed into loam types of soil is lost in 5 years, and most of the remaining 10% is oxidized to dieldrin, possibly by soil microorganisms.

Heptachlor behaves similarly, since two thirds of its residue is converted to heptachlor epoxide in the same period. The average half-lives for these chlorinated hydrocarbons in loam soil are 10 months for aldrin, 25 months for DDT (which is not degraded), and 10 months for lindane (although half of what is left consists of nontoxic products). Toxaphene is also detoxified at an appreciable rate.

The rate of loss of these chlorinated hydrocarbons is much less when the soil is dry, when it is under vegetation, and during the winter. It is greatest when the application is only on the soil surface and when moisture increases the mobility of the insecticide from one soil particle to another. The most powerful agent for the removal of soil residues is the wind, which can increase the loss by as much as 10 times. It is possible that the principal fate of these chlorinated hydrocarbons is volatilization; however, this dispersion may be reinforced when contaminated dust particles are blown away by the wind. Mold organisms, such as *Streptomyces* spp., and other Actinomycetes, can degrade DDT to TDE similar to the conversion effected by the bacteria *Proteus* spp., *Escherichia* spp., and *Aerobacter* spp. in the alimentary tract of mammals. Organophosphorus compounds, such as parathion and diazinon, are rather persistent in soil, particularly when it is dry or poor in microorganisms, while some of them, such as phorate, may be converted to even more toxic compounds.

Many OP compounds, when abundant in soil, reduce the growth of crop plants such as corn as much as do high concentrations of lindane or carbaryl. However, the usual accumulations of aldrin or heptachlor are harmless to plants and soil microorganisms, and technical DDT may actually stimulate plant growth. DDT and the cyclodiene-type insecticides can enter into root crops, especially carrots. Lindane readily enters seeds, but translocates with difficulty. When sprayed onto foliage, especially from emulsions or solutions, DDT may enter the waxy plant cuticle, where it is gradually dehydrochlorinated or otherwise degraded. DDT residues on and in orange rind have a half-life of about 50 days, but on alfalfa, into which it is scarcely absorbed, the half-life is 7 days. The OP compounds resemble nicotine and rotenone in penetration of plant tissues. Parathion readily enters the rinds of oranges, where it is metabolized with a half-life of 2 months, while the half-life of malathion is 1 month. The surface deposit of each, however, has a half-life of only 1 week. The half-life of fenitrothion, a less hazardous relative of parathion, was less than 1 day on rice, since it is rapidly metabolized through *p*-nitrocresol and phosphoric acids.

The truly systemic insecticides are translocated in the sap stream after being absorbed into the leaves and twigs. Many OP compounds, such as schradan, demeton, mevinphos, disulfoton, and phosphamidon, have this property. These insecticides, along with phorate, but not schradan, may be absorbed from the soil; schradan, demeton, and dimethoate may be painted on smoothed tree trunks; and dimefox [*O,O*-diethyl *S*-(β-diethylamino) ethylphosphorothioate hydrogen oxalate] (Tetram) and 3-(dimethoxyphenyloxy)-*N,N*-dimethyl-*cis*-crotonamide (Bidrin) can be injected into the trees. Mevinphos is rapidly metabolized by hydrolysis at the carboxyester and later the phosphate bond, its half-life being only 1 to 2 days. Dimefox is removed from the transpiration stream partly by hydrolysis and partly by volatilization, its half-life being approximately 3 days. Schradan is oxidized by the plant to the active insect toxicants (namely, the amidoxide or methylol methoxide of schradan) and subsequently degraded to ineffectiveness in 30 days. Demeton, methyl demeton, disulfoton, and phorate are almost completely metabolized in 1 month by oxidation to the respective sulfoxide toxicants, and later more slowly to sulfones and phosphates. Dimethoate is oxidized to the phosphate in the plant, a process analogous to the parathion–paraoxon conversion in the insect.

Chlorinated-hydrocarbon insecticides in warm-blooded animals are deposited in the fat of body tissues, especially the omentum or visceral fat. When their diet contains 100 ppm of DDT, mammals may accumulate up to 500 to 1,000 ppm of DDT in their body fat, at which level a balance is struck with detoxification and excretion. The principal metabolite is DDA [2,2-bis-(*p*-chlorophenyl) acetic acid], an oxidized metabolite that is excreted in the urine in amounts of 0.5 to 5% of the DDT ingested. There is some production of DDE in the tissues and some true excretion of DDA and DDT from the body tissues into the feces, which would be in addition to the unabsorbed DDT that passes out in the feces. Female mammals accumulate more DDT than males and secrete it in their milk at approximately one tenth of the concentration existing in their body fat. DDT applied in the field or forest does not affect mammals until the dosage exceeds 5 lb/acre. Shrews and mice are the first to show symptoms, and DDT dust has been used as a rodenticide in buildings. Birds begin to be affected at a dosage of 3 lb/acre, the first effect being on nestlings, because of DDT contamination of their insectan food. Nesting adults have been killed by the DDT dosage of 2 lb/tree applied to control bark beetle vectors of the fungus causing Dutch elm disease, *Ceratocystis ulmi* (Buisman) C. Moreau. The only food supply to survive consisted of earthworms, which then contained about 80 ppm of DDT and 30 ppm of DDE, derived from the contaminated soil they ingested. About 100 such earthworms constitute a lethal dose for the American robin, *Turdus migratorius* Linnaeus.

Methoxychlor, although quite toxic to fish, is virtually nontoxic to warm-blooded animals and is readily metabolized. TDE is another safe analogue, which is metabolized to DDA by mammals.

TDE can accumulate in fish without killing them; it thus becomes a hazard to fish-eating birds. The deaths of a considerable number of the western grebe, *Aechmophorus occidentalis* (Lawrence), on Clear Lake, California, have been associated with the application of TDE at 0.02 ppm to the lake water for gnat control three times during a 10-year period. TDE accumulations were 5 ppm in the plankton, 800 ppm in the visceral fat of plankton-feeding blackfish, *Orthodon microlepidotus* Greaser, 1,600 ppm in that of predacious large-mouth black bass, *Micropterus salmoides* (Lacepede), and 1,600 ppm in the western grebe. DDT commences to be toxic to young fish, especially in shallow water, at 0.2 lb/acre. Accumulations of DDT in the visceral fat of trout surviving forest-area spraying at 1 lb/acre reach approximately 5 ppm, but may range up to 200 ppm. Trout embryos, however, are particularly susceptible to DDT residues; an accumulation of only 3 ppm causes failure to hatch. There is evidence that DDT is metabolized by fish, and DDE appears in the body fat.

The cyclodiene derivatives, such as aldrin, dieldrin, and heptachlor, accumulate in body fat and are toxic even to mammals at field dosages down to 0.2 lb/acres. They are very stable, but slight dietary contaminations of aldrin (about 0.1 ppm) can be almost completely detoxified by the Norway rat, *Rattus norvegicus* (Erxleben). Toxaphene is more readily broken down, but it may accumulate in the body fat and in the food-chain organisms. Fish-eating white pelicans, *Pelecanus erythrorhynches* Gmelin, American egrets, *Casmerodius albus* (Linnaeus), and gulls on the Klamath Refuges of California have been killed by toxaphene draining from agricultural land into ponds to give the following maximal residues: algae, *Daphnia* spp., and snails, 0.2 ppm; small fish, 3 ppm; large fish, 8 ppm; and fish-eating birds, 40 ppm. In England, wheat seed treated for the control of the bulb fly, *Hylemya coarctata* Fallen, with aldrin, dieldrin, and heptachlor killed the wood pigeon, *Columba palumbus* Linnaeus, and ring-necked pheasant, *Phasianus colchicus* Linnaeus, that ate the seed; hawks that ate the pigeons were also killed. Dietary contaminations of 10 ppm of these cyclodiene derivatives can lower the total reproductive success of birds such as the bobwhite or quail, *Colinus virginianus* (Linnaeus), by reducing the egg lay, hatch, and nestling survival. Field applications of lindane, however, have no toxic effect on birds. Mammals metabolize this compound quite rapidly to trichlorobenzenes and phenols, which are excreted and thus do not accumulate much lindane in the body fat.

Many of the OP compounds seldom give rise to persistent residues in animals. Field applications of parathion or phosphamidon have reportedly killed birds by direct contact or by absorbing the toxicant through the feet, but malathion has been intensively applied to citrus orchards in Florida and forests in California without any noticeable bird mortality. Malathion is so rapidly metabolized by warm-blooded animals that it is virtually nontoxic to them. However, some species of fish are rather susceptible to malathion, and fenthion can accumulate as residues in fish fat. Among the carbamates, the insecticide carbaryl does not produce toxic residue in animals, but it is very hazardous to the honey bee, *Apis mellifera* Linnaeus.

INSECTICIDE APPLICATION

SELECTION OF APPROPRIATE INSECTICIDES AND FORMULATIONS

The selection of an appropriate insecticide in a given situation should be based on a number of principles; the most important is accurate identification of the pest insect. In some cases it may be necessary to obtain the services of a taxonomic specialist to obtain such a determination (see Chapter 2). When an identification has been made, a suitable insecticide may be selected from published recommendations of a given area or region.

Efficacy

Most of the insecticides now on the market are broad-spectrum chemicals that are effective against a great many species of insects and mites. Insecticides recommended by federal and state entomologists are usually the most satisfactory of a number of possible choices. The label of the packaged insecticide lists the insects that may be controlled by that chemical.

Compatibility

When two or more chemicals can be mixed together without any adverse change in their insecticidal activity or phytotoxicity, they are said to be compatible. In selecting combinations of insecticides or fungicides, or both, it is important to know what reactions might occur when the components are combined.

There are three principal kinds of incompatibility. First, there is a chemical incompatibility in which the chemicals react to form different compounds. For example, fungicides or adjuvants that are strongly alkaline may decompose synthetic organic insecticides and result in greatly altered activity. In the second kind, neither of the insecticides is toxic to plants when applied separately, but, when they are combined, a phytotoxic mixture is produced. An example of this is the mixture of lead arsenate and lime sulfur. The lime sulfur reacts with the lead arsenate to release arsenic oxide, which is soluble and very toxic to plant tissues. A third kind of incompatibility has to do with formulation problems. Such a problem occurs when oil and water do not mix, despite vigorous agitation. This is a physical incompatibility. When an emulsifier is added, the oil and water become physically compatible, usually with agitation.

Phytotoxicity

When an insecticide applied for insect control causes damage to the host-plant tissues, it is said to be phytotoxic.

It is not surprising that chemicals having biological activity, as evidenced by their toxicity to insects, might also be toxic to other living organisms, including plants. Many insecticides are phytotoxic, but at thresholds generally well above those required for insect control.

The susceptibility of plants to chemical injury varies greatly, as shown by the marked selectivity of herbicides, and the same principle applies to insecticides. A case in point concerns dinitrophenol compounds, which are used both as insecticides and herbicides.

In addition to differential susceptibility between species of plants, there may be differential susceptibility between varieties. For instance, the apple variety McIntosh is susceptible to injury by parathion early in the season at levels commonly employed for insect control, but other varieties are not injured at comparable concentrations. The susceptibility to insecticides of a given plant species is also influenced by factors such as growth stage, rate of growth, temperature, humidity, and other environmental factors.

It is advisable to accept the principle that the margin of safety of insecticides to plants is limited; therefore, these chemicals should be applied with due regard to the factors influencing phytotoxicity. For instance, certain petroleum oils are phytotoxic, but the factors accounting for phytotoxicity are now so well known that several types are available that can be applied with relative safety. The dinitrophenol compounds also can be employed with safety, despite their early record of phytotoxicity. Figure 41, however, illustrates severe injury to peach leaves, caused by spraying with 4,6 dinitro-*o*-cresol during warm weather.

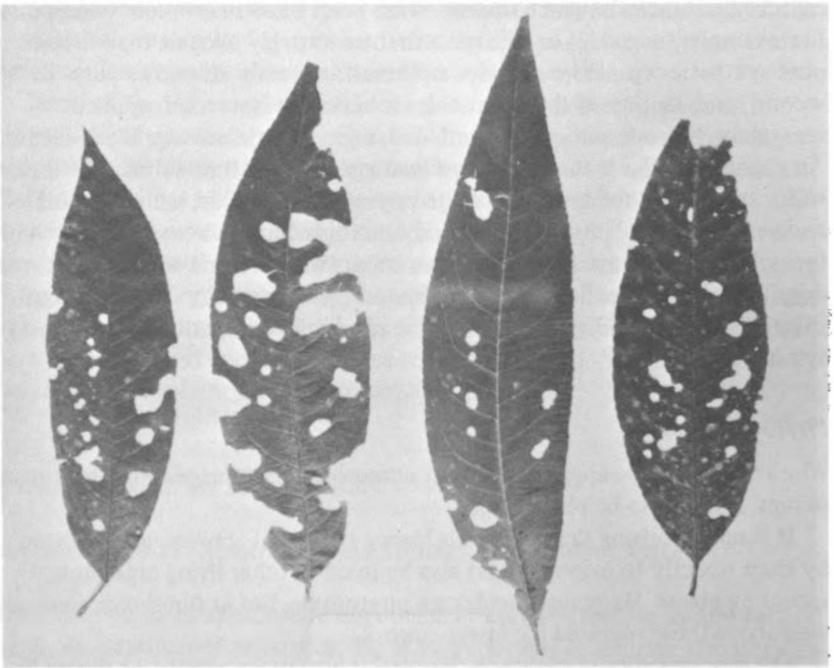


FIGURE 41 Phytotoxic effect of spraying peach foliage with 4,6-dinitro-*o*-cresol during warm weather. (From Ohio Agricultural Research and Development Center)

Phytotoxicity may be acute, as evidenced by immediate killing of tissue, or it may be chronic because of interference in physiological processes that reduces the efficiency of the plant. The use of certain types of oils on citrus has under some conditions reduced yields, although no outward manifestation of injury was evident. Some of the synthetic organic insecticides induce physiological changes in the plant in such a way that fruit-set is affected. Accordingly, the insecticide carbaryl is used as a thinning agent to reduce the set of apple fruits. In seeking maximum plant efficiency, the possibility of acute, chronic, or subtle physiological injury by insecticides should be considered. The phytotoxicity of insecticides is given careful consideration in the developmental stages prior to marketing a compound, and the precautions required for safe use are generally well known. Exactitude in terms of concentration, time of treatment, and other factors influencing phytotoxicity needs to be accepted as an essential feature of chemical control practices.

Insect Resistance to Insecticides

The problems related to the control of insect populations resistant to insecticides are among the most difficult facing entomologists today. When an insect population develops resistance to a given material, it is usually cross-resistant to related chemicals. Thus, in order to control the resistant population, an insecticide in a different class must be selected or a different method of control should be used.

Joint Action of Chemicals

Some insecticidal chemicals have the property of greatly increasing the toxicity of certain insecticides. The effect produced when two or more insecticidal agents are combined and the total effect is greater than the sum of the action of each of the agents used alone is known as joint action potentiation, or synergism. One of the most common examples of synergism results from the use of piperonyl butoxide in combination with pyrethrins. Nearly all aerosol formulations of pyrethrins contain piperonyl butoxide as a synergist. Activation is a special case of synergism, where a substance with no toxicity at the dosage employed increases the effect of a toxicant. Synergism is important because it may reduce the cost by providing more efficient insecticidal control; however, it may also enhance the mammalian-toxicity problem of the chemicals.

Persistence

Insecticides vary greatly in the length of time they are effective following application. Insecticides such as tepp hydrolyze rapidly in water and may not be effective for more than a few hours after application. Other compounds, such as aldrin or dieldrin, when applied to soils, may be effective for more than 10 years. The organic phosphorus insecticides are mostly nonpersistent chemicals, but the organic chlorinated hydrocarbons are persistent.

Whenever possible, a nonpersistent insecticide should be selected, in order to prevent long-lasting environmental contamination. However, persistent insecticides, such as aldrin, dieldrin, chlordane, and heptachlor, provide very economical control of soil pests for long periods; for example, white grubs, *Phyllophaga* spp.; grubs of the Japanese beetle; grubs of the northern masked chafer, *Cyclocephala borealis* Arrow, and the European chafer, *Amphimallon majalis* (Razoumowsky); and subterranean termites.

Side Effects and Food-Chain Involvement

In selecting an insecticide for a given problem, the possibility of undesirable side effects must be considered very carefully. An example of this is the spraying with unusually high concentrations of DDT for control of the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham), which transmits the fungus causing Dutch elm disease. If these high concentrations of DDT must be used to protect trees surrounding fish ponds, one may expect fish to be killed. In such situations the trees should be treated with a less toxic material.

Many insecticides are hazardous to honey bees and to other pollinating insects. Damage to bees can be minimized by taking the following precautions: (1) avoid drift of the insecticide into apiaries or bee yards and to adjacent crop or wild plants in bloom; (2) notify beekeepers at least 48 hours before treatment of large acreages, so that measures can be taken to protect the bees; (3) use an insecticide that will control the pest but is least toxic to honey bees; and, (4) if a chemical highly toxic to honey bees must be used, apply it during hours when bees are not visiting the plants. Where possible, insecticides should be chosen that are effective against the pest population but that have minimal effects against nontarget beneficial species, such as insect parasites and predators.

Undesirable side effects may also result when persistent insecticides become involved in the food chain of certain species. For example, the recommended spray for controlling elm bark beetles is 8 gal of 25% DDT emulsifiable concentrate in 100 gal of water. This is approximately 16 times the normal concentration used for most pests. DDT is comparatively stable and therefore accumulates in fairly high concentrations under the drip line of treated trees.

Earthworms, which are quite resistant to the toxic effects of DDT, may accumulate high concentrations of this insecticide in their fatty tissues. Robins, *Turdus migratorius* Linnaeus, and other birds that include large numbers of earthworms in their diets are less tolerant of the DDT, and may be killed by eating the worms. In such situations, the loss of songbirds must be weighed against the loss of elms, *Ulmus* spp.

Another aspect of pesticides is the breaking of food chains. In the control of black flies, for example, other aquatic insects that serve as food for certain fish, birds, and other animals may be drastically reduced. Thus, if the food chain is broken, lack of food may jeopardize the lives of many species of animals.

Available information also indicates that systemic insecticides can at times be indirectly toxic to predators, and possibly to some parasites, consuming prey on treated plants.

Selectivity

The physiological aspects of this general subject have been discussed under "Specificity." The following discussion relates to ecological considerations in the selective control of pests, such as time and place where one species may be exposed to treatment while others may not, consideration of habits as well as habitats, and choice of pesticides and types of formulations.

The possibility of selectivity based on time of occurrence of a pest and its location on the plant deserves careful consideration. Limiting the time of treatment or restricting the placement of insecticide can often achieve marked selectivity. Tobacco hornworms can be controlled by restricting treatment to the upper one third of the plant, since the immature leaves are preferred by larvae; this avoids disruption in the insect complex on other parts of the plant. Treatments for control of the European red mite, *Panonychus ulmi* (Koch), may be restricted to the semidormant period when eggs of the mite are exposed to treatment and most of the other species of mites and insects are in hibernation elsewhere and thus escape treatment.

The kind of pesticide and the type of formulation can also be used to advantage in controlling pests selectively. The chlorinated hydrocarbons, DDT and lindane, are generally ineffective against mites, and most applications of these materials actually allow an increase in mite populations. This is particularly true in the treatment of fruit trees and many ornamental plants. In these cases it may be advisable to include an acaricide in combination with a chlorinated hydrocarbon. Certain hydroxylated or sulfur-containing DDT analogues, such as Dimite, ovex, and dicofol, have been very effective acaricides.

Another example of the importance of formulation lies in the incorporation of pesticides with attractants that are highly selective in the attraction of a given insect to a bait.

Habit, as well as habitat, also is involved in specificity. The larva of the oriental fruit moth, *Grapholitha molesta* (Busck), for instance, usually does not swallow the first bite before entering a fruit, and by this act it avoids poisoning by stomach action. Once the worm is inside the fruit, it is protected from insecticides.

Economic factors are important, since industry's return on its investment in development requires high sales volume, which is best achieved by broad-spectrum insecticides that have multiple uses. It seems certain that advancing knowledge of molecular toxicology will open new possibilities for development of selective insecticides. Economic considerations should be tempered by the realization that higher-priced selective insecticides may in the final analysis be more economical than cheaper nonselective ones. Tremendous "maneuverability" exists in selecting insecticides with narrow spectrums of activity, directing insecticides to restricted areas, and timing their application to advantage.

Other Factors

Some other important factors to be considered in the selection of an insecticide for a given problem are the crops and uses for which the insecticide is registered by the manufacturer, the cost and availability, the appropriateness of the formulation for use in available equipment, and suitability for use in integrated control programs. (The last is a most important consideration and needs more attention.)

TIMING AND FREQUENCY OF APPLICATION

Timing of Applications

To obtain maximum control, insecticidal formulations are generally applied in one of two ways, the best way being determined on the basis of thorough knowledge of the life history and development of the pest and plant host under varying environmental conditions. (1) An application may be recommended when the insect pest first appears, or when a population reaches a certain level in an indicator trap, or when a certain number is present per unit of area. This kind of timing necessitates a careful assessment of insect and mite populations in the field, usually at not more than weekly intervals. (2) An application may be recommended at a particular stage of development of the host plant and pest as a result of a response of both to temperature. Examples of plant stages with respect to orchard pest sprays are dormant, delayed dormant, prepink, pink, bloom, petal fall, preharvest, harvest, and postharvest. The application to be made at a particular stage requires the observation of plant development every 3 or 4 days. When warmer than normal temperatures prevail, observations should be made more often.

Accurate timing of insecticidal applications is essential for effective pest control. In preventive control programs, an attempt is made to maintain a toxic residue on the plant or animal to protect it from insect attack. In corrective control programs, insecticidal applications are made only when a pest population reaches or exceeds the level at which it will begin to cause damage of economic importance. Integrated control programs may utilize preventive or corrective control programs, or both, as the needs dictate (see Chapter 17).

Nearly all pesticide recommendations applicable to food and feed crops and to livestock have a time limitation in regard to harvest or slaughter. This time limitation is expressed as the minimum number of days from the last application to harvest or slaughter. The time limitations are based on need for control and assurance of human safety with respect to treated crops and animals. If the time limitations are not observed, it is possible that insecticidal residues remaining on agricultural products will exceed established tolerances and be subject to governmental confiscation.

Frequency of Insecticide Application

The frequency of insecticidal applications depends on the insect species involved, the insecticide selected, and other factors, such as temperature, precipitation, humidity, and the rate of plant growth. For example, applications of such short-lived chemicals as tepp must be made daily for control of the adult periodical cicada, *Magicicada septendecim* (Linnaeus). Conversely, one application of aldrin to the soil will protect a lawn from Japanese beetle grub attack for at least 10 years. In plant protection, successive applications are usually made at intervals of 7 to 10 days. In the early part of the growing season, when plants are growing rapidly, application intervals may need to be shortened to 3 to 4 days.

INSECTICIDES IN COMBINATION WITH OTHER PESTICIDES AND FERTILIZERS

Insecticides are often applied on plants, such as fruits and vegetables, in combination with acaricides and fungicides to protect the crop from attack by insects, mites, and fungi.

Insecticides are sometimes applied at the same time as fertilizers; such operations are quite economical. For example, soil insecticides, fertilizers, and seed corn may be applied simultaneously, but usually they are not mixed together. This combination provides essential mineral nutrients and protects the roots of the plant from attack by insects such as the northern corn rootworm, *Diabrotica longicornis* (Say), the southern corn rootworm, *D. undecimpunctata howardi* Barber, and the western corn rootworm. Another example is the application of a mixture of soil insecticide with a lawn fertilizer to beautify and protect lawns.

Insecticides are seldom applied in combination with herbicides; however, this is an area deserving further investigation, since certain combinations are feasible. Plant growth-regulator types of herbicides, such as 2,4-D (2,4-dichlorophenoxyacetic acid), and 2,4,5-T (2,4,5-trichlorophenoxyacetic acid) should never be used in sprayers normally employed for insecticides. The herbicides contaminate the sprayers to such an extent that they cannot be used safely to treat desirable plants. It is therefore advisable to provide separate sprayers for herbicides and insecticides unless it is known that there is no herbicidal contamination problem.

DISPERSAL PROBLEMS DURING AND AFTER APPLICATION

Drift in Air

As a general rule, the application of insecticides should be avoided when the wind is blowing faster than 8 mph. Some air movement is helpful in dispersing insecticides. High and shifting winds, however, can cause an uneven distribution of the insecticide on plants and, more importantly, allow the insecticide to drift away from the target areas to contaminate the environment. The best time for spraying or dusting is usually in the early morning or late evening when there is little or no wind. To minimize harm to bees and other pollinating insects, the best time to apply pesticides is in the very late afternoon when the insects have stopped flying. Early-morning applications, although not quite as safe as those made in late afternoon, are much less dangerous than daytime treatments, which are to be avoided.

There are a number of factors that influence the movement of particles discharged from insecticidal application equipment. Some idea of the drift pattern of various particle sizes can be obtained from Table 7.

The drift of insecticidal sprays to nearby crops or livestock should be avoided. This problem is especially critical when applications are made by air. Do not allow poultry, dairy animals, or meat animals to feed on plants or drink water contaminated by spray or dust drift. The drift of an insecticidal spray onto a crop for which no use is registered may result in confiscation of the crop.

Dusts Dusting with insecticides has a greater drift hazard than spraying and results in less active chemical deposit on the plants. Dusts are most useful for special coverage problems, such as dense foliage on vines and in orchards where a significant crop depth is involved. Dusts are also popular on low-growing

TABLE 7 Drift Pattern in Relation to Particle Size

Drop Diameter (μ)	Particle Type	Distance in ft Particle Would Be Carried by a 3-mph Wind While Falling 10 ft
400	Coarse aircraft spray	8½
150	Medium aircraft spray	22
100	Fine aircraft spray	48
50	Air carrier sprays	178
20	Fine sprays and dusts	1,109
10	Usual dusts and aerosols	4,436
2	Aerosols	110,880

crops such as young cotton, where coverage under the leaf is desired; this coverage is difficult to obtain with sprays.

Sprays A wide range of chemical formulations is available in spray applications, and the spray particle size can be altered to fit application needs. With the new application techniques in low-volume and ultra-low-volume spraying, the problem of drift in the air will become intensified.

Dispersal in Soil and Water

Surface Movements Pesticides may be dispersed into soils and water resources by direct application or by drift during application to nearby agricultural areas. They may also be washed or blown in from the entire watershed. Much of the water pollution by pesticides comes from chlorinated hydrocarbon insecticides, particularly DDT and dieldrin.

Leaching Pesticides in general have little tendency to leach downward and laterally in the soil. This is particularly true of the chlorinated hydrocarbons and those organic phosphates that persist to any great extent. Soils, especially clays and those high in organic matter, tend to hold pesticides by sorption. The movement of the pesticides is usually associated with the movement of soil particles, but it also may result from the redisposition of volatilized molecules.

DDT applied on top of the soil tends to remain in the top inch of soil over a long period of time unless it is cultivated deeper into the soil. Groundwater is not contaminated to any significant extent as it passes through a DDT-treated area.

APPLICATION EQUIPMENT

The effectiveness of any spray program depends on the following application principles: the selection of the proper insecticide, application at the proper time, and use of equipment that will provide the most satisfactory coverage without contaminating the surrounding environment. Improper or inadequate consideration of any of these factors will result in an unsatisfactory control program. One of the major considerations in any spray program is the calibration and maintenance of pesticide application equipment. It is most important that the recommended dosages by used to avoid excessive residues, possible phytotoxicity, and contamination of surrounding areas and crops. The following discussion is concerned, in general terms, with the types of application equipment available for use by commercial agricultural interests as well as by private individuals in the United States.

Hydraulic Sprayers

The basic principle involved with hydraulic spray equipment is the use of water as the means of transporting the pesticide to the target area. The normal procedure is to mix the pesticide with sufficient water to obtain the desired rate per 100 gal or per acre at a specified pressure and speed. The liquid mixture is then forced through the spraying system under pressure and released on the target area.

Multipurpose Sprayers Multipurpose sprayers have been developed to provide the versatility needed to meet varying spraying requirements in diversified farming operations. The sprayers have a relatively wide pressure range to accommodate low-pressure requirements for spraying weeds and certain vegetable crops, as well as high-pressure application requirements for treating fruit trees, ornamentals, and livestock. Release of the spray is usually by means of a hand gun or boom.

Conventional Low-Pressure, Low-Volume Sprayers Low-pressure, low-volume sprayers are designed primarily for the control of insects and weeds where pressures up to 100 psi are adequate for coverage of the vegetation. Pesticide application is made through a boom equipped with nozzles or with a boomless cluster of nozzles. Application is made at rates up to 50 gal of spray per acre, in amounts adequate to cover the crop but not to the point of runoff, as used in full-coverage treatments (see Figure 42). Several types of ultra-low-volume sprayers are being developed for control of insects and weeds; they apply pesticides at rates as low as a few ounces per acre. The term "ultra-low-

FIGURE 42 Hydraulic low-pressure, low-volume sprayer. (From John Bean Division, FMC Corporation)

volume" spray is used when the total volume is ½ gal or less per acre and is undiluted. Highly concentrated pesticides and certain technical materials can be applied with this technique. Basically, sprayers of this type consist of a series of solid-stream nozzles that meter a concentrated pesticide formulation onto pairs of rapidly spinning stainless-steel disks or cages. The liquid is forced through the nozzles by compressed air in the container holding the liquid pesticide. Each pair of spinning disks is powered by a 12-V electric motor, which turns at 6,000 rpm. When the concentrated pesticide hits the whirling disks, it is broken into droplets. The pairs of disks are arranged so that the pesticide splashing off one disk immediately hits another and is dispersed.

High-Pressure, High-Volume Sprayers High-pressure, high-volume sprayers commonly called hydraulic sprayers, are used by growers of fruit and truck crops. These sprayers provide pressures of 100 to 600 psi and are rated in terms of gallons per minute of spray discharged by the pump at a certain pressure. They are designed to give thorough coverage to fruit and shade trees in full foliage, as well as to dense-growing bush, vine, and truck crops. Sprays are usually released by means of a boom or hand gun. Some manufacturers provide spray-head attachments for orchard and row-crop spraying, or booms equipped with drop-pipes or swivel connectors for use in vegetable or other row crops. Application rates of 200 to 600 gal/acre are commonly used (Figure 43).

Air-Blast Sprayers

The principle of the air-blast sprayer is based on the utilization of energy from a blast of air to propel sprays, in contrast to the use of large volumes of water for this purpose in hydraulic sprayers. Thus, in sprayers of the air-blast type, only relatively small volumes of water are required in spraying operations—a

FIGURE 43 Hydraulic high-pressure, high-volume sprayer. (From John Bean Division, FMC Corporation)

FIGURE 44 Air-blast sprayer. (From John Bean Division, FMC Corporation)

real economic advantage where adequate water supplies are not available. Basically, air-blast sprayers are designed to inject small droplets of spray material through nozzles into an air stream from a powerful fan that carries the spray to the target area. The air within the area to be treated must be displaced by the incoming spray-laden air. Displacement of air by air-blast sprayers ranges from a few thousand to over 100,000 ft^3/min at wind velocities up to 150 mph. Pesticides may be made up as dilute semiconcentrate or concentrate sprays. Application rates may vary from several hundred gallons of spray per acre to as little as 3 oz when utilizing ultra-low-volume equipment (Figure 44).

Row-crop sprayers, orchard sprayers, and mist sprayers are examples of air-blast sprayers. Although machines vary with respect to intended use, size, pump capacity, pressure, velocity of air stream, and cubic feet per minute air capacity, they all involve the principle of using an air stream to carry a pesticide in liquid form.

Dusters

Dusters also utilize the principle of an air stream to carry the pesticide to the target area. The basic difference is that the pesticide, instead of being dissolved or suspended in water, is impregnated on a suitable carrier, such as talc, calcite, clays, silica gel, calcium silicate, or diatomaceous earth, and then introduced into the air stream (Figure 45).

Aerosol Generators

Aerosol generators, or "foggers," are designed primarily for treating enclosed spaces and must in general be considered as space applicators. There usually is very little residual protection afforded by this type of pesticide application. These machines disperse extremely fine particles of pesticides into the air, where they remain airborne for a considerable period of time. Droplet breakup is accomplished by either thermal or mechanical means or a combination of both. Aerosol pesticide applications are effective against airborne insects, because air currents carry the pesticide to the target area, taking advantage of the principle of air inversion. Applications are usually made at night, when wind, temperature, and humidity conditions are optimum. Aerosol generators are commonly used for mosquito and fly control in dairy barns, area control of mosquitoes, and certain other pest-control operations (Figure 46).

Granular-Insecticide Applicators

Granular-insecticide applicators are designed to place pesticides impregnated on a suitable carrier, such as corncob, vermiculite, clays, or walnut shells, in the target area. Although variations in design occur, basic granular applicators consist of a hopper for the pesticide, a mechanical-type agitator at the base of the hopper, and some type of metering device, usually a slit-type gate, to regu-

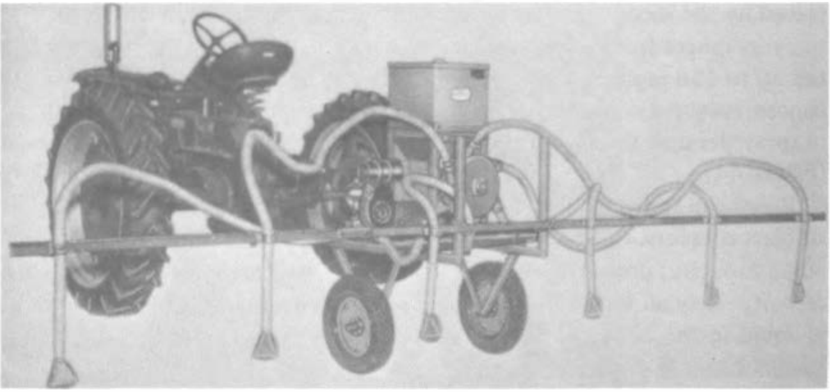


FIGURE 45 **Tractor-mounted power duster for row-crop treatments. (From Root-Lowell Manufacturing Company)**

FIGURE 46 Aerosol generator or fogger. (From Michigan State University)

late the flow of the granules. Granules may be applied as a broadcast or band treatment before or at planting time and worked into the soil; as a postplant side-dress application through drop tubes and fertilizer shoes; or from the air to penetrate foliage, and over water in mosquito-control programs (Figure 47).

Aircraft Application

Basically, aircraft application of pesticides, either from fixed-winged planes or helicopters, utilizes a modification of conventional low-volume, low-pressure hydraulic spray, dust, or granular application techniques. The most common dispersal apparatus used on aircraft is the pump, boom, and nozzle spray system. Spray-deposit patterns are adjusted by shifting nozzle locations on the boom. Droplet size can be varied by changing the pump pressure, changing the orifice size in each nozzle, or changing the nozzle direction in the slipstream of the aircraft. Application rate is changed by increasing or decreasing the nozzle size or the number of nozzles in the boom (Figures 48 and 49).

Once the spray, dust, or granular pesticide is discharged into the slipstream of the aircraft, it is carried by the flow of air displaced by the airplane in flight. the flow of air spreads backward, outward, and downward from the airplane.

FIGURE 47 Granular-insecticide applicator mounted on a four-row planter. (From Gandy Company, Inc.)

Rotary-type spray systems, or modifications of this idea, have been used on aircraft to obtain more uniform spray-droplet sizes. Such a system includes disks, brushes, or screens spun by small, wind-driven propellers or electric motors. Spray liquid flows to the center of the unit, either by pump or gravity feed, and sprays out by centrifugal force. Droplet size is decreased by rotating the device faster and is increased by reducing the speed of the unit. Rotational speed is controlled by adjusting the pitch of the propeller or by voltage regulators.

A recent development in ultra-low-volume spraying is the use of small rotary atomizing nozzles, such as the air-driven "Mini-Spin." There are several other similar devices, some of which are power driven. The rotary atomizing nozzles are particularly effective because they deliver a more uniform spray-droplet size, compared with the more conventional type of nozzle (Figure 50).

Hand Application Equipment

Hand-operated sprayers, dusters, and aerosol applicators are suitable for applying pesticides around the home and garden, in public and commercial buildings,

FIGURE 48 Fixed-wing airplane with boom-type sprayer. (From Michigan State University)

and on the farm. Hand-operated equipment is usually designed for applying pesticides to small areas.

Intermittent and Continuous-Pressure Sprayers Two types of hand-operated household sprayers of the atomizing type are available. Each sprayer consists of a tank, nozzle, pump, pump rod, and pump handle. The intermittent sprayer discharges spray material with each forward stroke of the pump. The continuous-type pressure sprayer continues to discharge spray as long as the pump is being operated. The sprayer may have either twin nozzles, one for fine sprays and one for coarse sprays, or an adjustable nozzle. Intermittent and continuous-type sprayers are designed for applying space or knockdown sprays to kill flying insects.

Aerosol Bombs An aerosol bomb is, essentially, a self-contained sprayer. It consists of a pressurized can or tank with a discharge valve and nozzle at the top. The insecticide is discharged from the can by means of a gaseous propellant included in the tank at the time of manufacture. Aerosol bombs are designed to apply space sprays for the control of flying insects or residual

FIGURE 49 Helicopter with boom-type sprayer. (From Bell Helicopter Company)

sprays for the control of household and certain other pests. The difference in principle between aerosols and other sprays is that a high percentage of each drop of spray leaving the nozzle is a gas at atmospheric pressure. It evaporates immediately after release, thus greatly reducing the size of the individual droplets as compared with conventional sprays.

Compressed-Air Sprayers Compressed-air sprayers consist of a 1- to 5-gal tank, air pump, filler cap, discharge tube, hose, spray-control valve, extension tube, and nozzle. Aqueous solutions, emulsions, or suspensions of pesticides are placed in the tank, the air-tight filler cap is put in place, and the air pressure pumped up to 30 to 50 psi. Wettable-powder suspension may settle out in the tank if allowed to stand for long periods. Occasional shaking of the tank will prevent settling. This type of sprayer is satisfactory for most spraying around the home. Some models of the compressed-air sprayers are fitted with refillable CO_2 cylinders that eliminate hand pumping and provide a constant pressure when spraying. One cylinder of CO_2 will usually expel three or four tankloads of pesticide.

Knapsack Sprayers Knapsack sprayers are carried on the back by means of a shoulder harness. Tanks average about 5 gal in size and are made of galvanized steel, copper, or stainless steel. Spray pressures of 30 to 100 psi are obtained by either a piston or diaphragm pump and are maintained by an airtight air-pressure chamber. On some models of knapsack sprayers, a double-acting slide-type trombone pump may be used to expel the liquid pesticide from the tank.

Bucket, Barrel, and Wheelbarrow Sprayers Basically, bucket, barrel, and wheelbarrow sprayers all consist of a pump, a pump handle, a spray hose, spray-control valve, extension tube, nozzle, and possibly an air-pressure tank to maintain constant pressure while spraying. They differ only in the container from which the pesticide mixture is pumped. Pressures up to 250 psi can be developed, the amount depending on the kind of unit. These units are suitable for spraying larger areas or for larger trees, because of the increased pressures.

Hose Sprayers Hose sprayers are designed to be connected to the garden hose. They consist of a jar for holding the concentrated mixture, a spray gun attached to the lid, a suction hose in the pesticide jar, and a shutoff valve on the gun. The spray gun meters the pesticide mixture from the jar by suction through

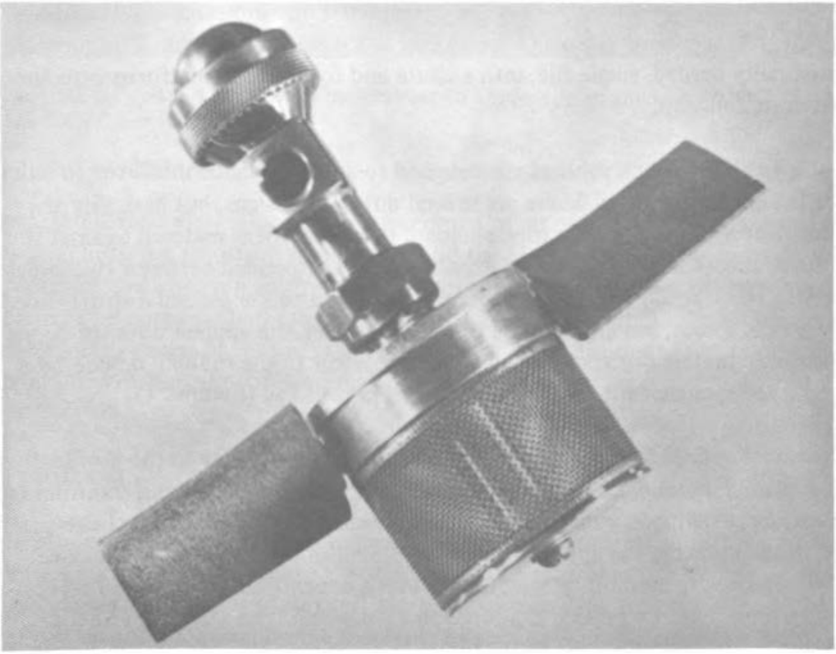


FIGURE 50 "Mini-Spin" unit for ultra-low-volume sprays. (From Michigan State University) venturi jets and mixes it with the water flowing through the hose. This type of unit is limited to the areas that can be reached by the garden hose. The distance the pesticide mixture can be sprayed depends on the water pressure. These units are suitable for spraying moderate-sized shrubbery, flowers, lawns, and vegetables, as well as barns and other buildings.

Dusters There are many types of pesticide dusters commercially available for the homeowner in the United States. They range in size from self-contained package dusters through knapsack dusters to wheelbarrow and traction-type dusters. They range in hopper capacity from a few ounces to 25 lb. Basically, they all depend on air to carry the insecticide to the target area. Air velocity to carry the dust may be created by simple plunger action, or by hand crank, chain, or belt-driven high-speed gears attached to a rotary fan or blower. The capacity of the air blast and size of the dust hopper limit the extent of use for each type of duster.

Animal Pesticide Applicators

Dipping Vats Dipping vats are used for the control of several species of pests affecting domestic animals. They are constructed of various materials but are basically designed to submerge the animal in a pesticide solution. The animals are usually herded, single file, into a chute and forced off a platform into the pesticide solution.

Back Rubbers Back rubbers are designed to apply pesticide mixtures to animals for the control of pests. There are several different designs, but basically they consist of a cable, chain, or rope enclosed in an absorbent material against which animals rub. The rubbing device may be loosely suspended between two poles or may be attached to a central pole and anchored to the ground a short distance away. Pesticides, usually in an oil or fuel-oil carrier, are applied directly to the absorbent material or transported from a reservoir to the rubbing device by a wick-type arrangement or dispensed from a porous bag (Figure 51).

Pour-on Applicators Pour-on applicators are used primarily in the application of systemic insecticides to control cattle insects. Animals receiving treatments involving systemic insecticides are usually herded, single file, into a chute past the person making the application with a dipper or similar calibrated device. The appropriate amount of insecticide, which depends on the size and weight of the animal being treated, is poured along the backbone (top line) of the animal.

Face-rubber Applicators Face-rubber applicators are specialized rubbing devices developed primarily to control the face fly, *Musca autumnalis* De Geer,

FIGURE 51 Rubbing device or back rubber for application of animal pesticides. (From The Dow Chemical Company)

on cattle. Basically, these applicators consist of an umbrella to which a curtain is attached. An absorbent material around the hem of the curtain contains the pesticide, which is replenished from a central reservoir by a wick-type arrangement. The entire system usually encloses a salt block, so that when cattle push their heads under or through the curtain to lick the salt, their faces come in contact with the pesticide-impregnated hem of the curtain.

FUMIGANTS

In modern terminology, a "fumigant" is a volatile chemical that is introduced into a confined space or into the soil to produce a gas that will destroy insect pests or other noxious organisms. The gaseous condition provides the property of diffusion which enables the fumigant to penetrate into masses of tightly packed materials or into small cracks and crevices in a structure. At the end of the time required for effective control of a given pest, aeration of the material or structure is started, and the gas diffuses away into the surrounding atmosphere until it is completely dissipated.

Flexibility in application is an important feature of fumigation as a modern method of pest control. In addition to treatments in conventional chambers, it is possible to control pest populations *in situ* in carriers such as ships, trucks, railroad cars, portable–demountable tents (Figure 52), or by sealing up buildings or covering them with gasproof sheets. For the purpose of soil fumigation, low-vapor-pressure fumigants may be injected into extensive areas of ground, or smaller areas may be covered with "gas-impervious" sheets and treated with more volatile gases. Space-fumigant operations of considerable size are often undertaken. Recently, in Florida, a 4-acre complex of airport buildings, including hangars, was covered with gasproof sheeting (Figure 53) and fumigated with sulfuryl fluoride to control dry-wood termites, which had become established in all parts of the complex, inside and out, including roof sheathing.

The use of fumigants is not confined to warm or hot conditions. Some fumigants have been used at temperatures as low as 0°C. As the temperature is lowered, however, the dosages and exposure periods have to be progressively increased, and post-fumigation aeration may be considerably prolonged.

From the point of view of practical application, fumigants may be divided into two main classes: high-vapor-pressure and low-vapor-pressure compounds. The former class includes materials of low molecular weight that are used to

FIGURE 52 A portable–demountable tent for commodity and nursery-stock fumigation. (From Canada Department of Agriculture)

FIGURE 53 A 4-acre complex of buildings being covered with gasproof sheeting prior to fumigation. (From The Dow Chemical Company)

fumigate commodities or to penetrate quickly and effectively into cracks and crevices. This group includes methyl bromide, ethylene oxide, hydrogen cyanide, and hydrogen phosphide (phosphine). The latter class consists of low-pressure compounds with higher molecular weights, which tend to volatilize and diffuse slowly. Advantage is taken of this property to provide varying degrees of persistence, which may be desirable for certain applications such as the treatment of storage grains that are not completely gastight, and for soil fumigation. Good examples of low-pressure grain fumigants are ethylene dibromide and ethylene dichloride, which are usually mixed with carbon tetrachloride to aid distribution in the grain mass.

Sorption and Residues

Fumigants are retained in or on fumigated materials by the action of forces generally referred to as "sorption." Physical sorption, as the name implies, is a purely physical reaction and is usually reversible at the time of aeration, following treatment. Its intensity varies inversely in proportion to the temperature of the surroundings. However, such sorption can result in the retention of the vapors of the fumigant in treated material. With low-vapor-pressure fumigants, such an effect may sometimes create a problem. For instance, there was a marked diminution in the size and number of eggs laid by hens that consumed grain that was not sufficiently aerated following fumigation with ethylene dibromide.

Chemisorption implies an irreversible reaction between the fumigant and the commodity that results in the formation of a chemical residue, which may be of significance in human or animal consumption. This reaction varies directly with temperature.

Concentration x Time Products

The treatment required to kill a given pest may be expressed in terms of concentration x time ($c \times t$) products. Except at extreme limits against a given pest, the relationship $c \times t = K$ holds with many fumigants to give predictable results. The amount or dose of fumigant introduced into the fumigation system gives no guidance to the actual effects being produced, because sorption by the commodity, and the structure or actual leakage, may result in a rapid loss of the original or "nominal" dosage.

Now that accurate and readily operated instruments, such as the thermal-conductivity analyzer (Figure 54), are available for determining concentrations in both the free air space and the load as a fumigation proceeds, it is possible to determine at any time the concentration of toxicant actually surrounding the offending organism. This takes guesswork out of the supervision of a fumigation, which may be terminated once the desired $c \times t$ product has been achieved.

Important High-Vapor-Pressure Fumigants

Methyl Bromide, CH_3Br (boiling point 3.6°C) Methyl bromide is today the most widely used fumigant. It is, for all practical fumigation purposes, nonflammable. Its powers of penetration enable it to be used on a very wide range of materials, including living plants, fruits, vegetables, stored grains, and processed foods. It is somewhat reactive chemically, and, with certain species of plants or fruits, it may produce physiological effects of varying intensity. Nevertheless, according to reliable estimates, 95% of nursery stock and other plants being moved in commerce are tolerant to treatments controlling the attendant insect pests. In foodstuffs, inorganic bromides are formed that are the object of residue tolerances in many countries. There is no evidence at present that the methyl radical (CH_3) of the molecule produces significant effects in fumigated foodstuffs.

Methyl bromide is also a useful fumigant for disinfesting empty storage spaces, such as warehouses and the holds of ships, as well as soil.

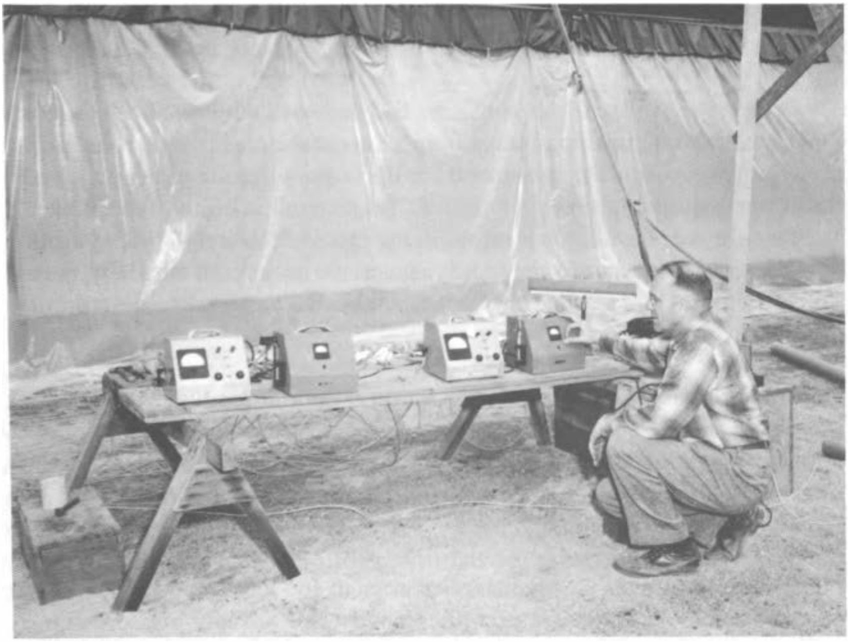


FIGURE 54 Thermal-conductivity units being used to determine the concentration of gas in various areas of a building under fumigation. (From The Dow Chemical Company)

Phosphine (hydrogen phosphide), H_3P (bp –87.4°C) Phosphine has come into prominence in recent years as a fumigant for grains in storage, seeds, and processed foods. It is very readily dispensed from pellets, tablets, or sachets containing aluminum phosphide, which reacts with the moisture in the air to yield phosphine and leaves a small residue of aluminum hydroxide, which must be eliminated. Phosphine itself is highly flammable, but in practice the pellets or tablets contain ammonium carbamate, which, at the time of application, yields ammonia and carbon dioxide in sufficient quantities to prevent combustion of the phosphine. As far as is known, the residues of phosphine are very slight and of no toxicological significance following routine aeration procedures.

Hydrogen Cyanide, HCN (bp 26°C) HCN was the first fumigant to be generally applied. Despite the fact that it has been largely replaced by methyl bromide and phosphine, it still has many uses. It is very soluble in water with the formation of a dilute acid, and must be applied with caution to living plants, fruits, vegetables, and many foodstuffs. It is strongly sorbed by many materials, and, in the slow process of desorption, may present toxic hazards. It is still useful for fumigating dry foodstuffs, grains, and seeds. With most foods there is little chemisorption, and the residue problem chiefly concerns the elimination of the actual fumigant vapors.

Ethylene Oxide, $(CH_2)_2O$ (bp 10.7°C) Ethylene oxide is one of the few fumigants toxic to both insects and microorganisms at reasonably low concentrations, but the $c \times t$ products required for the latter group are usually higher than those required for insect control. Ethylene oxide is highly flammable, and for many applications it is mixed in the ratio 1:9 by weight with carbon dioxide. It is fairly reactive chemically, and in use with foodstuffs it may result in the formation of chlorohydrins or the partial or complete destruction of certain vitamins.

Sulfuryl Fluoride, SO_2F_2 (bp 55°C) Sulfuryl fluoride is a highly penetrating and comparatively nonreactive fumigant that has been useful for control of termites in buildings. It is not presently recommended for use with foodstuffs.

Mixtures Containing Low-Vapor-Pressure Fumigants

Fumigant mixtures are largely marketed as grain and local "spot" fumigants in milling machinery. These mixtures often consist of low-vapor-pressure compounds in liquid form, which flow into the material, volatilizing gradually. In this form they are referred to as liquid fumigants. Some of the ingredients are flammable; therefore, other materials (sometimes insecticidal), that are nonflammable may be added to remove or reduce the fire hazard. Another reason for mixing is to dilute a principal toxic ingredient and aid in its uniform distribution in bulk material. Mixtures are also used as soil fumigants.

Some of the more important grain and local mill-machinery fumigant mixtures are:

1. Ethylene dibromide 7%, ethylene dichloride 29%, and carbon tetrachloride 64%, by weight. This is a grain fumigant designed for effectiveness in all grain storage-bin levels, especially the surface.
2. Carbon tetrachloride 80% and carbon disulfide 20%, by volume. By weight, these percentages would be 83.5 and 16.5, respectively. This fumigant, commonly called "80–20 mixture," has been used for treating grain for many years.
3. Ethylene dichloride 75% and carbon tetrachloride 25%, by volume, or 70% and 30%, respectively, by weight. This 75–25 mixture is one of the oldest grain fumigants and is still widely recommended.
4. Ethylene dibromide 70% and methyl bromide 30%, by weight. This is a space, mill-machinery, and recirculating grain fumigant. Another mixture contains ethylene dibromide 30% and methyl bromide 70%, by weight. This is a space and recirculating grain fumigant.

5. Carbon tetrachloride 57%, ethylene dibromide 20%, ethylene dichloride 20%, and inert ingredients 3%, by weight. This is a local milling-machinery or "spot" fumigant.

6. Acrylonitrile 20.64% and carbon tetrachloride 79.36%, by weight, or 34 and 66%, respectively, by volume. This is a space fumigant for tobacco storages as well as a milling, baking, and food-processing machinery fumigant.

The United States federal labeling laws require that the concentration of active ingredients be expressed as percent by weight. In common usage, however, the percentage figure often refers to percent by volume.

Soil Fumigants

Volatile pesticides are widely employed for the treatment of soil to control insects, nematodes, weeds, and harmful microorganisms. With the exception of methyl bromide, which has to be confined beneath gasproof sheets, these materials are usually applied as liquids or crystalline solids by means of specialized machinery (Figures 55 and 56). The distribution, action, and persistence of soil

FIGURE 55 Soil-fumigant applicator with a device for laying plastic film to seal in highly volatile fumigants. (From The Dow Chemical Company)

FIGURE 56 Soil-fumigant applicator for row treatments with low-vapor-pressure fumigants. (From The Dow Chemical Company)

fumigants are greatly dependent on the character and condition of the soil to which they are applied. Important soil factors are structure, compaction, organic-matter content, moisture, and temperature.

Some of the more important materials used for soil fumigation are:

1. Chloropicrin (trichloronitromethane). This is one of the oldest soil fumigants and is especially effective against soilborne plant-parasitic fungi. It also has nematocidal properties. It is used more widely in combination with other materials than by itself. Since it has strong lachrymatory or tear-gas properties, it is also used as a warning agent for fumigants such as methyl bromide.
2. Mixture of 1,3-dichloropropene and 1,2-dichloropropane. This mixture is widely used as a nematocide and insecticide. It is also used in combination with soil fungicides such as chloropicrin and methyl isothiocyanate.
3. 1,3-Dichloropropene and related chlorinated hydrocarbons. This is another widely used mixture with nematocidal and insecticidal properties. Like the previous mixture, it is used in combination with several other materials to provide more complete soil-fumigant properties.

4. Ethylene dibromide. This is a low-vapor-pressure soil fumigant with insecticidal and nematocidal properties. It is commonly used in combination with 1,3-dichloropropene and related chlorinated hydrocarbons.

5. Methyl bromide. This highly volatile fumigant possesses insecticidal, nematocidal, fungicidal, and herbicidal properties but must be used under a gasproof cover for best results. It is usually applied in combination with 2% by weight of chloropicrin, which serves as a warning agent for methyl bromide, which has no odor.

6. 1,2-Dibromo-3-chloropropane. This efficient nematocide is unique compared with most soil fumigants in that it can be applied in preplanting, at planting, and postplanting treatments for a wide variety of crops. It diffuses very slowly and thus provides nematocidal protection much longer than most soil fumigants. Its insecticidal properties, however, are very limited.

7. Sodium methyldithiocarbamate. This material is a water-soluble salt and is applied as a soil drench. Once applied, it converts in the soil to methylisothiocyanate, which is the active ingredient. When applied under proper soil conditions, it controls soilborne plant-parasitic fungi, nematodes, and certain insects; it also has herbicidal properties. Methylisothiocyanate is also used in combination with other soil fumigants, especially the mixture containing 1,3-dichloropropene and 1,2-dichloropropane. These combinations, like sodium methyldithiocarbamate, are useful in controlling the major soilborne plant parasites.

Application Equipment Many types of equipment are manufactured for the purpose of applying or injecting fumigants into the soil to control soilborne plant-parasitic nematodes, insects, fungi, or weed seeds. The selection of the type of applicator depends on the fumigant and the size of the area to be treated. In small areas to be treated with low-volatile liquids, the material may be applied with a soil-fumigation gun or poured from a can with two nail holes in the lid. Water-soluble drenches can be applied with a sprinkling can. Highly volatile materials, such as methyl bromide, can be applied quite easily with a simple applicator that punctures the 1-lb can and releases the gas through a length of plastic tubing under a plastic sheet for sealing-in the fumigant. Methyl bromide can also be applied easily and safely by attaching a plastic tube to a cylinder of gas and extending the other end into a building or a fumigation chamber, or under a plastic cover. The dosage can be determined by weighing the cylinder on a platform scale or by delivering the fumigant through a metering device attached to the cylinder.

Large areas may be treated with low-volatile liquids by means of chisel-type and plow-sole applicators. Granular and water-soluble materials can be worked into the soil with rototillers. The chisel-type applicator, which is the commonest type used, consists of a tank or cylinder for the fumigant (either liquid or gas under pressure), a metering device (pump, ground wheel, gravity-flow meter, or regulator valve), cultivator chisels mounted on a tool bar, and a device for sealing the fumigant in the soil (cultipacker, chain float, wood float, or plastic-cover tarp layer). Applicators are available for row and over-all or broadcast treatment (Figures 55 and 56).

One of the newer methods of application for fumigants with sufficient water solubility involves the use of a gravity-flow dispenser to meter the product through an irrigation pumping system.

Precautions for Safe Handling of Fumigants

All known insecticidal fumigants are toxic to man. Some, such as hydrogen cyanide, are immediate in their effect. Others, such as methyl bromide, may be slow-acting, so that symptoms of poisoning may not be apparent until many hours after exposure. If the necessary precautions are taken during application and subsequent aeration, fumigation is no more hazardous than many other aspects of modern technology. In some procedures it is advisable for those applying the fumigants to wear gas masks, fitted with the right kind of canister, both at the time of dispensing and at postfumigation aeration. A number of reliable devices are available for making spot checks of fumigant concentrations during and subsequent to treatment (Figure 54).

Some of the commonly used fumigants are highly flammable. Danger of fire, however, is often removed or greatly diminished by applying such a fumigant in mixture with another chemical that is nonflammable.

The use of fumigants should not be undertaken except by persons thoroughly trained in handling procedures; adequate gas-mask protection is essential for all operators involved. Compliance with all local municipal regulations is also highly important for the protection of the public.

INSECTICIDES AND HUMAN SAFETY

World War II was a turning point in the history of the development of pesticides. Prior to that time the available materials were a handful of general-purpose agents consisting principally of highly toxic alkaloids such as nicotine and strychnine; inorganic compounds of heavy metals such as lead, arsenic, and mercury, which have a high degree of chronic as well as acute toxicity; and a few botanicals such as rotenone and pyrethrum, which are less hazardous but of a more limited range of usefulness. The dangerous properties of most of these substances are well known from a century or more of clinical experience in the treatment of poisoning.

Since World War II a remarkable number of synthetic organic pesticides of many chemical types have been developed. Research chemists have had limited success in building molecular structures with predictable biological properties to meet specific needs. Many of these newer materials have been so widely accepted, and are used in such great quantities, that their possible long-term effects on the health of man has become a matter of public concern.

There is probably no other class of chemicals or drugs that has been so extensively studied, and about whose pharmacological and toxicological properties more is known. Much of this knowledge has been obtained from experiments on animals, and the question of whether reactions in humans will be similar to those observed in experiments is largely unanswered. However, animal data are reassuring. Data on human experience are equally reassuring. These include data on people occupationally exposed to amounts of the insecticides far greater than those to which the general public is ordinarily exposed. The final answer to some of the questions about chronic toxicity depends on many more years of use experience. Most of the questions on chronic toxicity are based on theoretical considerations, and there is little scientific evidence to support a prediction of deleterious effects from the continued responsible use of today's insecticides.

Any meaningful discussion of insecticides and human health must clearly recognize that there are three general types of exposure by which poisoning may occur: (1) incidental exposure during manufacture and use, which includes persons who handle the materials in the course of their occupations and individuals who use them in and around their homes; (2) accidental or deliberate exposure, including suicide, homicide, and ingestion by mistake; and (3) ingestion of contaminated food. The circumstances and problems associated with these types of exposure are quite different. Failure to distinguish between them has led to confusion in the public mind about the nature and extent of the problem of insecticide poisoning.

An even greater source of confusion is that no one is able to offer any reliable estimate of the incidence of nonfatal poisoning. Several factors contribute to this difficulty: (1) Except for the OP group, toxic doses of the synthetic pesticides often do not produce clearly defined, unique, or easily recognized clinical syndromes. Moreover, since the materials are new and of many diverse chemical types, physicians generally are not familiar with them. There is substantial evidence to suggest that diagnoses of insecticide poisoning are often made when that condition does not exist and frequently are not made when it does exist. (2) There is no generally accepted definition of the term "poisoning." It means different things to different people. There is a need for a standard against which the term may be applied. (3) In most of the United States, the reporting of nonfatal poisoning by insecticides is not required; therefore, there is no central registry of data.

Published estimates of morbidity from pesticide poisoning vary widely. The basis for most of them is the fatality rate, for which there are reliable data, multiplied by a factor. The most popular factor is 100, but this is admittedly a guess that has little scientific basis. Many believe that a factor of 100 is too high. In lieu of reliable morbidity data, death rates are commonly used as a measure of the poisoning problem. This is not without logic, because, with most of the materials under discussion, the principal problem is acute toxicity, and with many insecticides acute toxicity is high. There is undoubtedly a finite relationship between mortality and morbidity.

Practically all deaths from the newer organic pesticides are caused by two classes of insecticides: the chlorinated hydrocarbons and the OP group. Moreover, deaths from the organophosphates are four times as numerous as those from the chlorinated hydrocarbons, despite the fact that volume of usage of the chlorinated hydrocarbons is three times as large as that of the organophosphates. This is largely because, in terms of the single oral LD_{50} dose, many of the organophosphates are considerably more toxic than most of the chlorinated hydrocarbons. However, there are conspicuous exceptions in both groups.

All the organophosphates that have been registered by the U.S. Department of Agriculture (USDA) owe their insecticidal activity and their mammalian toxicity to their ability to inhibit acetylcholinesterase, an enzyme involved in neurotransmission. This is the only known action. Inhibition is a biochemical phenomenon that results in a transient impairment of nervous-system function. Illness from a toxic dose results in either death or recovery within a few days. There is no tissue damage. There are no residual effects, and chronic illness does not occur. An occasional claim has been made that these insecticides may cause chronic mental or nervous-system disease, but there is no sound evidence to support such claims.

The chlorinated hydrocarbons are central-nervous-system stimulants, although their mode of action is not entirely understood. The most characteristic manifestations of poisoning are muscle-twitching, tremors, and convulsions with or without nonspecific systemic symptoms. The clinical manifestations are usually of brief duration, after which the patient is apparently fully recovered. The qualifying term “apparently” is used because persons exposed to the chlorinated hydrocarbon insecticides in almost any quantity store them in the body fat. The concentration in fat appears to build up, with successive exposures, to a plateau, the height of which is related to the dose. Evidently, an equilibrium between absorption and excretion is reached. When exposure ceases, mobilization from the fat occurs slowly over a prolonged period, with subsequent degradation or excretion, or both. Fat storage of the chlorinated hydrocarbon insecticides has been a source of anxiety to many people. However, despite numerous careful and detailed studies, there is no evidence that it has any harmful effect. As with the OP compounds, chronic illness from this class of insecticides has not been identified.

With respect to the question of chronic exposure, it has been amply demonstrated that no one who lives in what is often referred to as a civilized community can avoid exposure to minute quantities of the chlorinated hydrocarbon insecticides. This is because of their widespread use and because they are stable chemical compounds that persist in our food and in our environment for long periods. Such minute exposures are responsible for the small accumulations that most people have in their body fat. Persons who repeatedly experience larger exposures, as in the course of certain occupations, build up higher concentrations in their body fat, but these also seem to be without deleterious effect.

With the organophosphorus insecticides, the case is quite different. These compounds are unstable under conditions of use, and they are readily decomposed by small amounts of alkali. Therefore, cumulative exposure occurs only in in persons who are exposed on a day-to-day basis. Under such circumstances, a progressive nonsymptomatic decrease of cholinesterase activity takes place, and the rate of decline is proportional to the degree of exposure. When enzyme inhibition has reached a critical level, acute illness occurs; this is identical in all respects to the illness that follows single large exposures. The OP compounds are not stored in the body; they are rapidly degraded and excreted.

Three fourths of the deaths from pesticides, and probably a similar proportion of poisoning cases, result from accidental or deliberate ingestion. More than half are cases in which children swallow the pesticide, usually in concentrated form. This is almost invariably a matter of easy accessibility resulting from adult carelessness. An important contributing factor is the deplorable practice of transferring the insecticide from the original container into an empty beverage bottle, where it is easily mistaken for a potable liquid. Most accidental poisoning by ingestion in adults occurs in this fashion. Fatalities from deliberate ingestion are estimated to account for 25% of all deaths from insecticides. The more toxic OP compounds, especially parathion, are usually used in the case of these fatalities.

No death has ever been reported from pesticide residues on food. In fact, there have been only two or three reports of illness occurring in this fashion, and these are instances of illegal residues resulting from improper agricultural practices.

Occupationally related cases occur through inhalation or skin absorption, or both. Occupational fatalities are mostly from the organophosphorus compounds. This class of pesticide is easily and quickly absorbed through the intact skin. Contact with the skin causes no irritation or discomfort, and the potential victim may therefore be unaware of the danger. Dermal absorption is the most important exposure factor in occupational cases. Poisoning in children through skin exposure is not uncommon. In such cases the child has usually been playing with an "empty" container of one of the more toxic phosphate esters. From the viewpoint of a health hazard, there is no such thing as an empty container.

With the OP insecticides, exposure via the respiratory tract is of lesser importance than skin exposure. With the chlorinated hydrocarbon group, the reverse is often the case. While many insecticides in the latter group readily pass through the dermal barrier, respiratory-tract exposure appears to be a more important avenue of entry.

In this discussion the term "inhalation" has been avoided. With few exceptions, the vapor pressures of insecticides of both types are so low that they constitute no hazard by vapor inhalation at ambient temperatures. Many of the OP insecticides contain mercaptan linkages, which give them a strong characteristic odor that is easily detected in very low concentration, but there is no relationship between odor and hazard.

In agricultural operations, any of the insecticides may be and usually are applied as either sprays or dusts. The equipment used in such operations produces particles, over a range of sizes, liquid or solid, of larger than respirable size, and they are airborne for only short periods. Therefore, the airorne particles do not enter the body of an exposed operator through the lungs but instead are caught up in the secretions of the upper respiratory tract and swallowed. In reality then, this is exposure by ingestion.

Toxicologically, insecticides are commonly classified by the numerical value for their single-dose oral LD_{50} in test animals. This figure usually refers to "technical" grade material; this means the undiluted insecticide of commercial quality. Most technical-grade insecticides contain a minimum of 95% active ingredient, and some run consistently over 98%. Therefore, the LD_{50} may be assumed to represent the toxicity of the pure chemical as indicated in Table 8.

TABLE 8 Acute Oral and Dermal LD_{50} Values of Insecticides for White Rats (unless otherwise indicated)[a]

	Oral LD_{50} (mg/kg)		Dermal LD_{50} (mg/kg)	
Insecticide	Males	Females	Males	Females
Chlorinated Hydrocarbon Insecticides				
aldrin	39	60	98	98
benzene hexachloride	1,250[b]	–	–	–
chlordane	335	430	840	690
chlorobenzilate	1,040	1,220	–	>5,000
DDT	113	118	–	2,510
dichloropropane–dichloropropene	140[b]	–	2,100[b,c]	–
dicofol	1,100	1,000	1,230	1,000
dieldrin	46	46	90	60
Dilan	600	475	6,900	5,900
endosulfan	43	18	130	74
endrin	17.8	7.5	18	15
ethylene dibromide	146	117	300[b-d]	–

TABLE 8—Continued

	Oral LD_{50} (mg/kg)		Dermal LD_{50} (mg/kg)	
Insecticide	Males	Females	Males	Females
ethylene dichloride	770[b]	–	3,890[b,c]	–
heptachlor	100	162	195	250
Kepone	125	125	>2,000	>2,000
lindane	88	91	1,000	900
methoxychlor	5,000	5,000	–	>6,000
mirex	740	600	>2,000	>2,000
paradichlorobenzene	>1,000	>1,000	–	–
Perthane	>4,000	>4,000	–	–
Strobane	200[b]	–	>5,000[b,c]	–
TDE	>4,000	>4,000	>4,000[b,c]	–
Telone	250–500[b]	–	–	–
toxaphene	90	80	1,075	780
Organic Phosphate Insecticides				
azinphosmethyl	13	11	220	220
Bidrin	22[b]	–	225[b,c]	–
carbophenothion	30	10	54	27
Ciodrin	125[b]	–	385[b,c]	–
Compound 4072	14.5	13	31	30
coumaphos	41	15.5	860	–
demeton	6.2	2.5	14	8.2
diazinon	108	76	900	455
dichlorvos	80	56	107	75
dimethoate	215	–	400	610
dioxathion	43	23	235	63
disulfoton	6.8	2.3	15	6
Dursban	163	135	2,000[b]	2,000[b]
EPN	36	7.7	230	25
ethion	65	27	245	62
fenthion	215	245	330	330
malathion	1,375	1,000	>4,444	>4,444
methyl parathion	14	24	67	67
Methyl Trithion	98	120	215	190
mevinphos	6.1	3.7	4.7	4.2
naled	250	–	800	–
Nemacide V-C 13	270	–	–	–
parathion	13	3.6	21	6.8
phorate	2.3	1.1	6.2	2.5
phosphamidon	23.5	23.5	143	107
ronnel	1,250	2,630	–	>5,000
Ruelene	635	460	–	–
tepp	1.05	–	2.4	–
trichlorfon	630	560	>2,000	>2,000

TABLE 8–Continued

	Oral LD_{50} (mg/kg)		Dermal LD_{50} (mg/kg)	
Insecticide	Males	Females	Males	Females
Carbamate Insecticides				
carbaryl	850	500	>4,000	>4,000
Zectran	37	25	1,500–2,500^{e}	1,500–2,500^{e}
Other Insecticides				
Aramite	3,900	3,900	–	–
binapacryl	63	58	810	720
calcium arsenate	–	298	–	2,400
cryolite	200^{b}	–	–	–
dinitrobutylphenol	40	40	150–200^{b,f}	–
dinitrocresol	31	31	300–400^{b,f}	–
dinitrocyclohexylphenol	60	60	>1,000^{b,f}	–
fenson	1,350–1,740^{b}	–	–	–
Genite 923	500^{b}	–	–	–
lead arsenate	–	1,050	–	>2,400
Lethane 384	90	–	250–500^{b,c}	–
metaldehyde	ca. 1,000^{b,g}	–	–	–
Morestan	1,800	1,100	>2,000	>2,000
nicotine sulfate	–	83	–	285
ovex	2,050^{b}	–	–	–
Paris green	–	100	–	>2,400
pyrethrins	>1,500^{b}	–	>1,880^{b,c}	–
pyrethrum	1,870	820	2,060^{b,c}	–
rotenone	50–75^{b}	–	> 940^{b,c}	–
ryania	1,200^{b}	–	>4,000^{b,c}	–
Sulphenone	1,400–3,650^{b}	–	–	–
tetradifon	>14,700^{b}	–	>10,000^{b,c}	–
Thanite	1,600^{b}	–	6,000^{b,c}	–

[a] Data from U.S. Dep. Agr. Handbook 331, Suggested guide for the use of insecticides to control insects affecting crops, livestock, households, stored products, forests, and forest products 1967. (Data assembled by the Pesticides Program, Public Health Service, U.S. Department of Health, Education, and Welfare. Most of the values were determined under standardized conditions by that program.)

[b] Sex not indicated.

[c] Value for rabbits.

[d] Approximate LD_{50}.

[e] Estimated LD_{50}.

[f] Value for guinea pigs.

[g] Value for dogs.

From a practical viewpoint, there is concern not only with the toxicity of an insecticide, but also with the hazard. Hazard means the possibility that a given substance will cause injury under practical conditions of exposure. A number of factors determine the hazard of an insecticide; toxicity is only one of them. The degree of dilution and the type of formulation are also important. Consider parathion as an example. It has an oral LD_{50} of about 13 mg/kg for male and 3.6 mg/kg for female white rats, but it is usually applied at concentrations of about 0.5%. Such dilution of the toxicant at time of application reduces the chance of overexposure. Thus, the LD_{50} of the material to which agricultural workers are exposed during actual application is 200 times the value usually given for parathion, or 720 to 2,600 mg/kg. At this dilution it is obviously a less hazardous material. Skin exposure to liquid formulations is more hazardous than to dusts, because a liquid permits more intimate contact of more skin with more material per unit of skin surface. Since the vapor pressure of most insecticides is very low, toxicity seldom results from inhalation of the vapor.

In recent years there has been so much publicity about pesticide hazards that much of the general public has developed a distorted impression of the magnitude of the problem. Vital statistics show that pesticides account for only 1 out of every 700 accidental deaths and only 5% of all poison deaths in the United States. As a cause of death, pesticides are far outranked by common drugs and by household agents such as cleaners, polishes, and solvents. For many years, the ubiquitous aspirin tablet has caused about the same number of accidental deaths annually in the United States as all the pesticides combined, and since 1957 aspirin has caused slightly more accidental deaths. As a matter of record, the death rate for all pesticides has remained constant at slightly over one per million of population for the past 25 years. Approximately two thirds of the deaths even now are caused by the pre-World War II pesticides. The synthetic organic compounds of the post-World War II era are rapidly displacing the older insecticides and, in volume of use, already exceed the latter by a factor of ten to one. Considering that the total pesticide usage in the United States today is five or more times higher than it was 25 years ago and that current usage of pre-World War II agents is less than one half of what it was then, experience with the synthetic agents apparently has been very good. If fatalities are related to usage volume, the current death rate from the pre-World War II pesticides is ten times that of the synthetic insecticides. If death rates were computed separately for the newer organic synthetics on the basis of the published data, the mortality rate in the United States would be about one death per 5 million of population.

Since many of these pesticides are highly toxic materials, the remarkably good safety handling record must be atrributed to the efforts of the regulatory agencies to prevent misuse and to the activities of manufacturers and of those concerned with public health to educate the public on the hazards and the safe use of these materials. The success of these efforts is confirmed by the low incidence of deaths in all circumstances of exposure except accidental and deliberate ingestion. The problem of the control of willful ingestion is an integral part of the problem of control of poisonings generally and is not peculiar to pesticides. Pesticide safety will be achieved only through a continuing massive effort to educate the public on the need for careful handling and the storage of all hazardous materials out of reach of children, pets, or livestock, and away from food or feedstuffs. further important safety considerations include: (1) using the correct pesticide at the recommended dosage for the job and only when necessary; (2) avoidance of inhaling pesticide sprays or dusts when mixing and applying them; (3) avoidance of spilling pesticides on the skin and clothing; (4) not eating or smoking when working with pesticides and doing so only after washing and changing clothes; (5) need for proper disposal of empty pesticide containers; and (6) probably most important of all, *read the entire label* on the pesticide container and follow the directions and precautions *exactly.* Little can be expected from more legislation and regulation, since experience has taught us that carelessness cannot be legislated out of existence.

PESTICIDE REGULATION AND REGISTRATION

The regulation of pesticides by government agencies is based on various laws that have as their intent the protection of the consumer with respect to product safety, quality, quantity, and performance according to the claims made.

All pesticides, including insecticides, that are shipped in interstate commerce in the United States, must be registered under the Federal Insecticide, Fungicide, and Rodenticide Act. Many states also have similar laws regulating pesticides sold within the boundaries of states. Registration under the federal law usually provides the basis for registration under a state law.

REGISTRATION PROCEDURE

To register a pesticide under the U.S. Federal Insecticide, Fungicide, and Rodenticide Act, the manufacturer submits an application for registration to the Pesticides Regulation Division of USDA's Agricultural Research Service. Basically, the application includes the following information:

1. A statement of the active and inert ingredients contained in the pesticide formulation.
2. A proposed label bearing the brand name of the products; an ingredient statement giving the percentage and description of the active ingredient, and the percentage of the inert ingredient; the claims and directions for use, which include the names of the pests to be controlled, the amount of pesticide

to be used, when it is to be used, and any precautions or limitations; a warning or caution statement, which, if complied with, is adequate to prevent injury to living man and useful vetebrate animals, useful vegetation, and useful invertebrate animals, and which includes the statement "keep out of reach of children"; the net contents of the package, and the name and address of the manufacturer, distributor, packer, formulator, or registrant. When the label is printed, it must bear the registration number assigned by the USDA.

3. If the use and claims for the pesticide are new, a full description of the scientific tests made to show the effectiveness of the pesticide and its safety to the host plant or animal to which it is applied.

4. A full description of the toxicity tests conducted on laboratory animals in support of statements designed to instruct the user on how to handle and apply the pesticide without injury to humans or animals. As a basic minimum these tests determine acute oral toxicity of the pesticide to laboratory rats; toxicity to rats on inhalation, if it is likely there would be exposure to vapors, mists, or dusts; toxicity to rabbits by skin absorption; and, usually, whether or not the pesticide will cause injury or irritation to the eyes of rabbits. If the pesticide is used under circumstances where wildlife will be exposed, additional information is needed to determine the effects on fish and wildlife.

If the pesticide is not proposed for use in or on food crops or animals, and the USDA concludes, after a study of the information presented, that the pesticide and the claims made for it are safe and effective, the Fish and Wildlife Service of the U.S. Department of the Interior, and the Food and Drug Administration (FDA) and the Public Health Service, both of the Department of Health, Education and Welfare (HEW), are notified of the USDA's intent to register the pesticide. These other agencies then have the opportunity to review the information. If they have no objection, the USDA informs the applicant that his pesticide is registered, and the manufacturer is then permitted to ship and sell his product. However, if the pesticide is to be used in or on food crops or animals, the manufacturer must submit detailed chemical analyses of any residues and delay registration until the FDA establishes a residue tolerance.

ESTABLISHMENT OF RESIDUE TOLERANCE IN FOOD

When the use of a pesticide on a raw agricultural commodity results in a residue on the food at harvest (or slaughter), such food is adulterated unless the residue is declared safe, exempted from the requirements of a tolerance, or is within the tolerance established under the Pesticide Chemicals Amendment of 1954 to the Federal Food, Drug, and Cosmetic Act, and also the Food Additives Amendment of 1958 if there is a concentration of the residue in processed food.

It is also necessary to establish a tolerance if the pesticide is to be used on a food crop or animal in a way that may reasonably be expected to result in small residues, even though they may not be detectable by existing analytical methods. This policy was instituted by the USDA and the FDA in 1966, when the so-called "no-residue" and "zero-tolerance" concept in the registration of pesticides was abandoned in favor of finite tolerances at the negligible level. The administration of the above Amendments is carried out by both the FDA and the USDA. To obtain a tolerance or exemption from a tolerance for a pesticide chemical in or on a raw agricultural commodity, a petition proposing a tolerance or an exemption is submitted to the FDA and the USDA. This petition contains:

1. The name, chemical identity, and composition of the pesticide chemical.
2. The amount, frequency, and time of application of the pesticide chemical.
3. Full reports of investigations made with respect to the safety of the pesticide chemical. These reports include detailed data derived from appropriate animal or other biological experiments.
4. The results of tests on the amount of the residue remaining, including a description of the analytical method used.
5. Practicable methods for removing any residue that exceeds the proposed tolerance.
6. Proposed tolerances for the pesticide chemical if tolerances are proposed.
7. Reasonable ground in support of the petition.

FUNCTIONS AND AREAS OF RESPONSIBILITY OF FEDERAL AGENCIES WITH RESPECT TO ESTABLISHING TOLERANCES

If a petition is found to be complete, it is filed by the FDA and acted on by both the FDA and the USDA. The functions and areas of responsibility of the Federal agencies involved follow.

The USDA decides questions of agricultural usefulness and appraises the analytical methods and the residue data.

The FDA decides questions of safety and appraises the data on residues resulting from the proposed use from the standpoint of the safety of the tolerance proposed. The basic authority to establish tolerances or exemptions from tolerances directs the Secretary of HEW to limit residues of poisonous or deleterious pesticide chemicals in or on raw agricultural commodities to the extent necessary to protect the public health. After the pesticide tolerance petition is filed by the FDA, the USDA examines the residue data and the information supplied on usefulness in the application for registration. If the data so indicate, the USDA certifies to the Secretary of HEW that the pesticide is useful for the purposes for which a tolerance is requested. The USDA also gives an opinion as to whether or not the tolerance or exemption proposed by the petitioner reasonably reflects the amount of residue likely to result when the pesticide chemical is used in the manner proposed for the purposes for which certification is made. The FDA then reviews the residue, metabolism, and toxicity data assembled from tests conducted on laboratory animals, which include long-term dietary feeding studies with rats and dogs and reproduction studies in laboratory animals. By the application of a large safety factor, the FDA scientists arrive at a judgment as to whether or not the residue tolerance as requested would be safe for humans. If safety is assured, the tolerance, or exemption from tolerances, is established by the FDA in a regulation published in the Federal Register. Following the establishment of the tolerance, the USDA registers the pesticide. Registrations must be renewed with the USDA every 5 years.

EXPERIMENTAL PERMITS AND TEMPORARY TOLERANCES

If a pesticide is to be used for experimental purposes on a large scale in field tests to determine its usefulness and limitations, it is possible to obtain a temporary permit from the USDA for bona fide experimental programs under the supervision of qualified persons. If the experimental pesticide is to be used on food crops or food animals and residues of the pesticide are likely to result, and it is desired to dispose of the crop or animals for food purposes, then it is necessary to obtain a temporary tolerance from the FDA, following much the same procedure as indicated above. Permits for experimental use and temporary tolerances are usually issued for a period of 1 year.

FOREIGN REGISTRATIONS

Many countries other than the United States have laws and regulations pertaining to pesticides. Some, including Canada, have requirements almost identical to those just described; others have rather simple registration procedures.

RESEARCH NEEDS

There are numerous opportunities for research in the insecticide field. Some of the major areas for investigation follow.

RESEARCH FOR NEW INSECTICIDES

There is a need for the discovery and development of entirely new groups of chemical insecticides and an extensive examination of the biochemistry of insect metabolism to facilitate such research. The insecticides presently available consist essentially of only four groups: certain botanicals; the chlorinated hydrocarbons, including the cyclodiene derivatives; the organic phosphates; and the carbamates. New groups of toxicants having a different mode of action are especially desirable. They should be of such a nature that the target insect could neither detoxify them nor develop resistance to them. Meanwhile, the investigation of insect metabolism, particularly the characteristics of insect esterases and their modification by mutant gene alleles, will show the mechanisms by which resistance develops and the ultimate fate of the OP and carbamate compounds.

Biologically labile, but physiochemically stable, insecticides are particularly needed. Possibilities in this respect may be found among the OP compounds. Such insecticides would retain the advantage of persistent residual effect but would lack the disadvantage of concentrated accumulation in organisms as they pass through food chains.

The broad-spectrum insecticides, although they have been most useful in the past, need to be partially replaced by insecticides specific against certain taxa or even single species of a pest. For this purpose, a new taxonomy based on the chemistry of the pest (chemotype) rather than on its appearance (phenotype) can be developed through the investigation of insect metabolism. The resulting refinements can greatly aid integrated control and substantially reduce hazards to man and wildlife.

STUDIES OF THE EFFECTS OF INSECTICIDES ON THE ENVIRONMENT

The use of pesticides in agriculture, forestry, and public health fields, either properly or improperly, may result in the contamination of the environment. It is inevitable that organisms other than pests in control programs will become exposed to pesticides. Conservationists, wildlife biologists, and various scientists responsible for the development and use of pesticides recognize the importance of this problem. Entomologists, in particular, have the difficult task of controlling insect pests that conflict with man's interests while protecting beneficial insects. Need for research on the effects of pesticides on insect parasites and predators, as well as on other desirable animals, should be emphasized. Information from such research should help us to avoid many of the unfortunate effects that may follow the use of insecticides and should be of great value in the design of integrated control or pest-management programs.

Although the fate of chlorinated hydrocarbon and other insecticides in the soil and water is becoming quantitatively characterized, considerably more information is needed on the extent to which these compounds are detoxified by microorganisms, plants, and various classes of animals.

There is a need for quantitatively establishing the connection between the level of residues found in the tissues of wildlife, particularly birds and fish, and any observed side effects on survival or reproductive capacity. It is vital to determine the danger point of accumulation, to prevent persistent insecticide residues from causing unanticipated damage to the biota. It is also very important to relate the amounts of residue in various parts of the environment in terms of hazards or lack of hazards to organisms existing in the environment. It is unfortunate that any conspicuous mortality of fish or reproductive failure of birds should be automatically ascribed to insecticides whenever any level of residue is found in their tissues. Such associations will remain purely circumstantial until the toxic thresholds of residues are established experimentally. This requires the colonization of wildlife species at research stations, so that they can be exposed to known amounts of insecticide and submitted to chemical assay on a predetermined schedule or as soon as symptoms of poisoning appear. The tedious gathering of residue data involved in a monitoring program would be meaningless unless the results are compiled into a universal system of figures for each insecticide, so that when taken in combination with the experimental results they may ultimately indicate the true position.

New and more efficient test methods and research approaches necessary for the understanding of the effects of pesticides on our environment suggest themselves. The proper utilization of all available modern techniques in all our sciences requires careful attention. Great care in the development of more specific analytical methods is needed for proper identification of pesticide residues that may contaminate our environment. It is highly important that monitoring and other cooperative research programs designed to appraise the significance of the amounts and effects of pesticides found in fish, wildlife, and other organisms be coupled with adequate investigations by competent scientists in all fields involved.

IMPROVEMENT OF APPLICATION TECHNIQUES AND EQUIPMENT

Application techniques and equipment should be further refined so that most if not all of a toxicant can be placed in the microenvironment of the pest. With such techniques, macroenvironment contamination would be minimized and there would be little or no deleterious side effects on nontarget organisms. The newly developed low-volume and ultra-low-volume applications of nonpersistent insecticides show promise of improving pest control. There is some question, however, concerning the magnification of certain deleterious side effects, and these should be investigated. The use of concentrates, along with the improved knowledge of drift control, should be considered in areas where insecticides are to be used. Equally important is the need for research and development of new types of application equipment.

Further research is needed to develop effective population sampling procedures. When these techniques are perfected, the optimum timing of applications in integrated and corrective control programs can be achieved.

FUMIGANT RESEARCH NEEDS

The roster of fumigants presently in use is reasonably adequate to deal efficiently with the range of problems generally encountered, but this temporary situation gives no excuse for complacency. All the commonly used fumigants have well-recognized limitations, and the search for new compounds or effective combinations of known compounds must be continued. The discovery and development of new fumigants may have to be undertaken largely by industry, which is best equipped to deal with engineering problems of manufacturing and handling highly volatile gases.

Our knowledge of the mode of action of fumigants against insects is very limited. In the past there has been considerable extrapolation from mammalian studies, but the mode of action in insects may differ somewhat from that of mammals. Laboratory work has been largely confined to the determination of comparative toxicities of various fumigants to different insects, based on mortality counts. There should be more research devoted to an understanding of the physiological responses of insects to fumigants and of the biochemical effects of the fumigants on the sites of action within the organism. Some progress has been made in recent years, but this whole field is still largely unexplored.

FORMULATION STUDIES

Intensive research is needed to provide more accurate data on the formulation and chemical stability of insecticides. This is an extremely important but frequently overlooked research area. More attention needs to be devoted to insecticide formulations with respect to (1) improving biological efficiency and compatibility with other pesticides, (2) reducing phytotoxic effects, (3) improving storage stability, and (4) improving the effects of diluents on biological activity in comparative tests under different climate conditions. In addition, new insecticides should be thoroughly tested to determine the suitability of their use in various types of application equipment. Studies should also be made on these new formulations to determine their usefulness in integrated control programs.

RESEARCH ON EFFECTS OF PESTICIDES ON HUMAN HEALTH AND SAFETY

Despite the vast body of knowledge that has been acquired on the human toxicology of modern pesticides and the epidemiology of poisoning, there are several gaps in our knowledge where intensified research effort might yield information of considerable practical value. Considerable progress has already been made by the study of persons with prolonged, intensive exposure, including those who manufacture or formulate pesticides. The results are compared with those found in the general population. However, it is important that this work be continued and systematized, as in fact is being done in laboratories established by the Public Health Service for this purpose in 16 states.

The need for sensitive methods for the detection of small amounts of insecticides in the body fluids, tissues, and excreta is also important. It is true that arsenic, lead, mercury, and 11 isomers or metabolities of six chlorinated hydrocarbon insecticides are regularly found in people of the general population. The concentration of these materials is greater in persons with occupational or other special exposure. In addition, at least nine other pesticides have been specifically identified and measured in the blood of persons with greater than ordinary exposure. However, methods should be developed for a great many other compounds to which people, especially formulators and farmers, may be exposed.

A great deal has been learned by testing blood cholinesterase activity in persons exposed to the more toxic organic phosphorus compounds. However, the results of these tests are difficult to interpret except in people who have had a single exposure. There is a need for better understanding of the test in persons with repeated exposure to organic phosphorus compounds. There is also a need for equally sensitive tests for the pharmacological effects of other classes of insecticides, whether these compounds can or cannot presently be measured in human tissues.

Progress in saving lives by the prevention of accidents caused by insecticidal application will be greatly assisted by additional knowledge of how accidents have occurred. Federal and international agencies should place more emphasis and coordination on the identification of these accidents.

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CHAPTER 17

Integrated Systems of Pest Management

Much of the material discussed in previous chapters has dealt with the principles involved in various individual methods of insect-pest control and management and with the tools and techniques available for making the methods effective. Each control method has an important place, but none has always provided a satisfactory solution to the many problems posed by insects and other arthropod pests. Dramatic successes can be cited for the different control methods, but equally dramatic failures have occurred. Problems have accelerated during the last two decades that demonstrate conclusively that single-factor, *ad hoc* approaches to the control of insects and related pests are inadequate.

An attitude of unreserved optimism became prevalent among most entomologists with demonstration of the spectacular effectiveness of DDT. Failures of synthetic organic insecticides to control all pests, and adverse consequences of their widespread use during the last two decades, have changed this attitude to a more rational but somewhat pessimistic one. Development of insecticide-resistant populations, resurgence of treated populations, elevation of secondary pests (or in some cases, previously innocuous species) to a status of primary importance, deleterious effects on populations of nontarget organisms, and general pollution of the environment with measurable residues of persistent chemicals pose increasingly critical problems associated with the use of synthetic organic insecticides.

Attempts to control pests by biological means have resulted in striking successes in some cases. Importation and dissemination of exotic parasitic and predacious insects, development and use of insect-resistant plant varieties, and dissemination of insect pathogens have given excellent control of a few species.

There are many insect problems, however, that cannot be solved by any one of these approaches.

The rapidly evolving problem of controlling insects and related pests suggests the probability of increasing difficulty. The unprecedented rate of increase of the the world population imposes the necessity for greater production to meet man's needs. Efforts to feed and clothe a population expected to double by the end of the twentieth century will force agriculture toward the comparative simplicity of monocultures, with their tendency toward encouraging violent oscillations in pest populations. Problems posed by such genetically plastic and evolutionarily resourceful organisms as insects and related arthropods and their interactions with a rapid changing agriculture are too dynamic to be solved by reliance on one-component control systems. Obviously, man is not making the best use of his ability to control insects in view of what is known about the factors governing the fluctuations of populations in nature. Man's efforts to impose his will on nature have amounted, until recently, to little more than what has been termed "bulldozing nature," with little thought to consequences. His efforts to control arthropod pests have sometimes resulted in as much harm as good. During the last few decades, substantial information has accumulated to suggest that pest control must be extended beyond empirical methods to a system based on principles of applied ecology. Such a system has been developing rapidly; it has come to be known as integrated control.

DEFINITION OF INTEGRATED CONTROL

Several definitions of integrated control have been proposed. They include:

1. Applied pest control that combines and integrates biological and chemical measures into a single unified pest-control program. Chemical control is used only where and when necessary, and in a manner that is least disruptive to beneficial regulating factors of the environment. It may make use of naturally occurring insect parasites, predators, and pathogens, as well as those biotic agents artificially increased or introduced.
2. An ecological approach to pest management in which all available necessary techniques are consolidated into a unified program, so that populations can be managed in such a manner that economic damage is avoided and adverse side effects are minimized.
3. A program of arthropod-population management designed to keep pest populations below economic tolerance levels by maximizing environmental resistance and supplementing this by use of selective pesticide applications if economic tolerance levels are threatened.
4. Utilization of all suitable techniques to reduce and maintain pest populations at levels below those causing injury of economic importance to agricul-

ture and forestry, or bringing together two or more methods of control into a harmonized system designed to maintain pests at levels below those at which they cause harm—a system that must rest on firm ecological principles and approaches.

All the proposed definitions have one common theme: the system must be based on sound ecological principles. Early definitions emphasized a two-component system based on biological and chemical control, and the concept of integrated control has come to be most frequently thought of as a blending of these two control techniques.

HISTORY OF INTEGRATED CONTROL CONCEPT

Integrated control is a new name for a philosophy and system of pest control that entomologists, particularly in forestry, have been using for years. When analyzed, successful control programs attributed to single factors are often found to have involved factors other than those deliberately invoked. Integrated control differs from past approaches in being a deliberately conscious attempt to blend and harmonize the different suitable techniques making up the control system to solve pest problems better.

Integrated control, as thought of today, began about 25 years ago in widely separated places: Germany, Nova Scotia, and California. Pickett and his co-workers in Nova Scotia stressed their conviction that ecological concepts and methods must be applied to the problems of controlling insects. By this they meant that a thorough understanding of the dynamics and ecology of pest populations would lead to a method of control that would rely not only on pesticides, but also on natural enemies. They advocated the development and use of spray programs that would have minimal harmful effects on beneficial species, which could then exert their full effects on the pest. They called this approach the modified program but eventually substituted integrated control, a term apparently first proposed by Bartlett in California in 1956. It is based on achieving maximum effectiveness of natural control agents already established in an ecosystem (rather than on introducing and disseminating exotic species) and in using, in addition, selective pesticide applications when necessary. At one time the program was being used on more than 80% of the apple and pear acreage in Nova Scotia, with notable success and drastic reductions in the cost of pest control. However, as a result of radical changes in economics and increased demand for blemish-free fruit, growers in the area have reverted to the traditional method of chemical control.

Integrated control in California owes its origin to the successful supervised control procedures worked out for alfalfa and cotton in the late 1940's. With supervised control, growers arrange for entomologists to check fields carefully and frequently and to recommend the application of pesticides only when pest populations are found to be increasing beyond the restraint of natural mortality factors in the environment.

A similar type of supervised control of forest insect pests had been practiced in Germany for more than 25 years. No control operations were started until the role of natural mortality factors had been carefully evaluated.The comparative sophistication of the supervised control program for control of forest pests is demonstrated by the fact that the first life tables for insects were published 35 years ago.

Coincident with these advances, much interest has been shown in the desirability of applying ecological principles to problems of controlling or regulating pests of importance to agriculture and forestry. This interest has contributed to clarification of thinking on the principles of pest control and to more precision and sophistication in the definition of objectives. The following points have been emphasized: (1) there is need to study the ecosystem as a whole, and pest control must become applied ecology; (2) the best methods of controlling pests can be devised only with a knowledge of the principles underlying the fluctuations in pest populations; (3) the control of populations is a function of the ecosystem, and a knowledge of all the principal elements of the system is essential to an understanding of population phenomena; and (4) fundamental work on the ecology of a pest, combined with studies of control methods, is ultimately more fruitful in reducing damage than the purely *ad hoc* approach.

EVOLUTIONARY PROCESS OF PEST MANAGEMENT

It is obvious from early papers that integrated control was developed as a concept of blending chemical and biological control techniques, and many workers still hold to the idea of a two-component system. In the early 1960's the first suggestions arose for broadening the concept to include the integration, not only of chemical and biological control methods, but of all practices, procedures, and techniques relating to crop production, into a single unified program aimed at holding pests at subeconomic levels. Thus, current thinking has evolved from the relatively narrow concepts of the two-component system—chemical and biological control—to the much broader concept of pest management.

Although integrated control by definition involves at least two components, some of the most successful efforts rest on only one factor. Two classic examples are control of the cottony-cushion scale, *Icerya purchasi* Maskell, by the vedalia, *Rodolia cardinalis* (Mulsant), and control of the grape phylloxera, *Phylloxera vitifoliae* (Fitch), by use of American resistant rootstocks with European grapevines, *Vitis* spp. Neither of these methods, the first biological control and the second control by use of plant resistance, has required the integration of any other technique to give outstandingly successful control of two important pests.

The concept of eradication of pest species from large areas of the world has gained much momentum during the last decade. It clashes with the concept of integrated control, i.e., a blending of biological and chemical methods. The difficulties of reconciling these two approaches are apparent from the intrinsic nature of biotic regulating mechanisms. The maintenance of such mechanisms depends on a continuous supply of hosts and proper environmental conditions. In general, the higher the economic level, the greater the possibility that biotic regulating mechanisms can come into play, and therefore the greater the opportunity for integrated control. In some pest-control situations the population levels that can be tolerated are extremely low or may even be zero. Satisfactory control is very difficult to achieve in any such case, and the very low economic levels usually create impossible goals for biological control and consequently for integrated control.

The necessity for utilizing economic levels of infestation as one of the basic principles of integrated control illustrates the conceptual conflict between two major schools of entomological thinking. One school adheres to pest control from an ecological basis, relies heavily on the two-component system (biological and chemical methods), and accepts the presence of subeconomic populations of pests as being prerequisite to the successful operation of such a system. The presence of pests in populations that are of subeconomic importance are thought of as being analogous to gasoline in an internal combustion engine. It is the fuel that provides the energy for operation of the system; without it the machine cannot function. It is this obvious dependence on the presence of subeconomic levels of pest populations for the successful operation of integrated control systems that forms the basis for the opinion of many entomologists that the concept of eradication is the antithesis of the concept of integrated control.

The philosophy of the second school is essentially the same as that of a great majority of modern farmers. It believes that the presence of subeconomic pest populations is undesirable, and that many pests, if not all, should be eradicated by the invocation of special techniques, or, if not eradicated, kept at the lowest possible levels by regularly scheduled applications of broad-spectrum insecticides.

Although eradication of a species is a concept as difficult to accept by those oriented toward the multidimensional concent of integrated control as is the necessity for maintenance of subeconomic infestation levels by many entomologists, it is recognized as a valid objective and reasonable goal in certain cases. Well-organized and properly executed eradication programs, armed with the necessary tools and proceeding from a base of thorough knowledge of the pest and its ecosystem, provide the ultimate solution to the problem of a number of noxious species. The successful program for eradication of the screw-worm, *Cochliomyia hominivorax* (Coquerel), is a classic example.

There is nothing ecologically abhorrent about the eradication of a species. The geological record shows that many species have become extinct. Some entomologists argue that it is morally wrong for man to attempt to eradicate something that he cannot create. Yet they do not deny man's right to attempt to control insect populations. In either case, the environment must be changed. Eradication projects are directed against pests that otherwise would be the target of other methods of pest control, and eradication may be the lesser of two evils in the ecological sense.

Perhaps a great deal of resistance to the eradication concept results from knowledge that many eradication attempts in the United States have failed and only a few have succeeded. Attempts to eradicate firmly established species by the application of broad-spectrum insecticides at high rates of application to huge areas have usually been unsuccessful. The consequences of such efforts in terms of adverse effects on nontarget organisms have often been detrimental. However, new concepts and improved tools of considerably greater sophistication than any previously known are receiving the attention of entomologists and other researchers. Prospects for their successful use justify a re-evaluation of the potential of eradication techniques for control of an invading species or of a species making significant extensions of its range.

The broad concept of integrated control that has evolved—a concept that includes use of all appropriate techniques, aptly described as a group of devices forming a network for serving a common purpose—allows reconciliation of the differences in the two philosophies. Integrated control systems by definition may lead in either of two directions—eradication or pest management. A combination of methods, acting concurrently or in sequence, may be used to reduce a pest population to very low levels, where special techniques, such as the use of sterility, may eradicate the population. More often, however, an integrated control system will reduce the pest to an acceptable level and then maintain it there—true management of pest populations.

Recently, the term "pest management" has been advanced as one more expressive of current thinking than "integrated control" as a reference to pest control from ecological bases. The term is much more inclusive than integrated control, and it avoids the conflict between proponents of integrated control systems that require the presence of subeconomic levels of pest populations and those who maintain that eradication measures can be harmonized with such a system. Pest management emphasizes the comprehensive nature of the approach and its reliance on ecological principles; it also conveys the idea of the intelligent manipulation of nature for man's benefit—the same kind of manipulation that is involved in fisheries and wildlife management and in the whole system of modern agriculture. Pest management, like integrated control, implies the continued existence of potentially harmful species at tolerable levels of abundance. However, it does not, by definition, imply that pests should not be eradicated whenever feasible, since the extermination of a pest species is likely to be the only completely satisfactory solution to many important insect problems.

The conceptual basis for this thesis rests largely on the principle that relative scarcity is more characteristic of phytophagous organisms than is great abundance, and that pest status is achieved as a result of man's activities. Man's upsets of long-established patterns of intraspecific and interspecific relationships are pest-inducing. Some of the most important and obvious of these activities are: (1) introduction of actual and potential pests to previously uninfested areas; (2) introduction of exotic plants and animals to new areas; (3) growing of improved varieties and strains of organisms; (4) intensive land use and practices of monocultures; and (5) simplification of the ecosystem as a result of agricultural and industrial activities.

Pest management is a system that seeks to deal with the abundance of populations by reducing the fitness of the innate qualities of individuals in a population for operative features of the environment. According to this concept, fitness can be reduced by (1) modifying the innate qualities that enable individuals to perform their life functions or (2) altering essential features of the environment to make it no longer able to support large numbers of a population, while leaving the innate qualities of its members unchanged.

Such a concept considers pest management as comparable with crop and wildlife management. It recognizes as a basic premise that it is only for the selfish welfare of the human being that there is any need for management of populations of any organism. Like integrated control, it recognizes that the future solution to pest problems may be in learning to live with pest species rather than eliminating them. It does not exclude single-factor and eradication techniques, and it avoids the semantic difficulties, implicit in the early concept of integrated control, of being a contradiction in terms. There is much to commend the term "pest management" as a description of the goals of economic entomology. If it were adopted, the term "integrated control" would refer only to ways in which various techniques are used to achieve pest management.

NEED FOR INTEGRATED SYSTEMS OF PEST MANAGEMENT

The rapid development of integrated-control techniques and their widespread acceptance during the last two decades have resulted from a growing awareness of the shortcomings of single-factor approaches to pest control. Rachel Carson was not the first to bring to public attention the obvious drawbacks of excessive reliance on and use of chemical pesticides to deal with problems of pest control. Her literary skill and emphasis on the sensational, however, made her criticisms especially effective. It is unfortunate that errors of logic and fact in her book have seriously eroded the impact of her message.

Sole reliance on chemicals for pest control has the following drawbacks: (1) selection of resistance to insecticides in pest populations; (2) resurgence of treated populations; (3) outbreaks of secondary pests; (4) residues, hazards, and legal complications; (5) destruction of beneficial species, including parasites, predators, and pollinating insects; and (6) expense of pesticides, involving recurrent costs for equipment, labor, and material.

Resistance is a problem in evolution; its development in a pest population is evolution in action. Some individuals in almost every population of pests possess more ability than others to detoxify a chemical and render it harmless or to escape its effects through changes in behavior. High levels of resistance to one or more insecticides occur in some isolated populations of normally susceptible species prior to their exposure to the chemicals. Resistance has been observed in about 220 major pests, including species of mites, mosquitoes, house flies, moths, and beetles. The continuing development of insecticide-resistant biotypes in other species is a virtual certainty. With some species the problem has already accelerated to a frantic race by entomologists to develop new pesticides in order to keep just one step ahead of the pests.

Resurgence is a phenomenon with roots in basic ecological principles. The ability of an organism to reproduce and increase is usually variable; in addition to the organism's genetic composition, one of the major factors influencing this ability is its own density. As density increases, competition for food and other requisites increases and reproduction decreases. If the population rises to extreme heights, reproduction may cease and the population may decline precipitously. At low densities, there is little competition, and reproduction is at or near its maximum for the existing environmental conditions. Thus, a pesticide applied to a high pest population may drive it to a low level where reproduction is great, with the result that the population surges back to its original high and damaging proportions. Pesticide destruction of beneficial parasites and predators that normally hold pest populations in check is often an important factor in resurgence. If, in addition to having a higher reproductive capacity at low densities, a pest is simultaneously freed from the restraint imposed on it by natural enemies, its resurgence or flareback will be that much more rapid.

The outbreak of pests other than those against which pesticides are directed is a common phenomenon. For example, the red-banded leaf roller, *Argyrotaenia velutinana* (Walker), increased in importance on apple in Ontario, Canada, from 1929 to 1956, from an insect of casual or even rare occurrence to one of the most serious with which fruit growers had to contend. During this period, spray programs became increasingly complex, starting with a simple program of lead arsenate and ending with very complex schedules of DDT, parathion, TDE, and malathion. The red-banded leaf roller, a secondary pest, rose to a position of primary importance as a consequence of a pesticide program directed against other species. The mechanisms involved in this phenomenon are not certain. It seems clear, however, that a factor of major importance was the destruction of parasites and predators by use of wide-spectrum pesticides.

It must be stressed that the use of chemical insecticides may change the status of pests in the direction of less importance, even to the extent that major noxious species completely lose pest status. Until about 1949, when DDT came into general use in northeastern Canada, the fruit-tree leaf roller, *Archips argyrospilus* (Walker), which had been the most abundant leaf roller on apple, often causing extensive damage, declined as rapidly as the red-banded leaf roller increased. At the same time that the fruit-tree leaf roller disappeared, populations of the oblique-banded leaf roller, *Choristoneura rosaceana* (Harris), and the three-lined leaf roller, *Pandemis limitata* (Robinson), declined precipitously. Similarly, the use of chlorinated hydrocarbon and organophosphorus insecticides for control of the boll weevil, *Anthonomus grandis* Boheman, in the southern United States resulted in a decline of the cotton leafworm, *Alabama argillacea* (Hübner), and the cotton aphid, *Aphis gossypii* Glover, from the status of major pests to that of relative obscurity.

Hazards to man of the widespread use of chemical pesticides have not been adequately evaluated because of insufficient information. However, there is no evidence that the minute traces of pesticides with which man is in daily contact injure or seriously affect him in any way. This is not the case with many species of wildlife, especially fish. There is ample evidence that substantial populations of various wildlife species in many areas have been destroyed or seriously harmed by contact with pesticides. The hazards from misuse of the more toxic chemicals are quite clear.

Cost is one of the most important drawbacks to excessive reliance on chemicals for pest management. Hundreds of millions of dollars are spent on pesticides each year in the United States, but statistics are poor on the value of the crop saved by the use of chemicals. The economics of pest control is discussed fully in Chapter 18.

One of the most pertinent facts about the comparatively high cost of pesticide programs is that substantial reductions can be made in the amount of chemicals being used for pest control without sacrificing efficiency. This can be done by (1) replacement of scheduled applications with applications based on population assessment, and (2) recognition that many crops can tolerate substantial levels of infestation of some pests without economic loss.

The general public, perhaps unfortunately, has been conditioned to demand food products totally devoid of blemishes produced by pests. Growers have been led to expect absence of all pests, which frequently is not required to prevent economic loss. The demand for such unnecessarily high efficiency in pest control has been further conditioned by the action of regulatory agencies in declaring that insects in food are filth or indicators of filth. These attitudes seriously handicap efforts to adopt pest-management systems that do not require excessive application of pesticides. As the advantages of such systems become better known, consumers may alter their attitudes and accept an occasional blemish.

These points illustrate the weakness of pesticides as strategic tools for pest control. It is now necessary to broaden this indictment somewhat and to point out that no single artificial control technique should be relied on exclusively for the regulation of pest populations. Because of their dynamic, adaptable nature, biological controls can sometimes be excluded from this indictment. In many cases, flexible and natural biological controls have proved permanent and highly effective, and further instances of this will undoubtedly be developed in the future.

Components of agricultural and forest ecosystems are continually evolving. A dynamic, multilateral management system for regulating pests in these changing situations is essential. Most one-component systems lack the flexibility necessary for the suppression of dynamic pest populations. Almost invariably, one-component systems lack permanence and in this sense are palliative rather than curative. The empirical approach to pesticide use usually relieves rather than cures; no matter how intelligently pesticides are used, they can never be more than palliatives. Moreover, many one-component systems create unwanted side effects, because they do not adequately recognize other components of the ecosystem and they tend to disrupt rather than to harmonize with them in advantageous ways. Unilateral systems exert pressures on pest populations from narrow bases and facilitate pest reactions by presenting a single plane of activity. Finally, most pest situations involve complexes of pest species, and this adds dimensions and demands normally beyond the scope of any one-component control system.

Although pesticides have been indicted on various valid grounds, the main drawbacks to their exclusive use, which arise from their great effectiveness, are based on the previous statements regarding the unsuitability of unilateral, one-component control systems. However, no individual control technique, and most emphatically this includes pesticides, should be rejected from consideration in integrated control systems. Each control technique has a potential role to play in concert and harmony with the others, and a major technique such as the use of pesticides can be the very heart and core of integrated systems. Chemical pesticides will continue to be one of the most dependable weapons of the entomologist for the foreseeable future. Rapid expansion of agriculture, in developing countries especially, will demand repressive applications of chemicals for pest control until more acceptable alternative techniques can be developed. There are many pest problems for which the use of chemicals provides the only acceptable solution. Contrary to the thinking of some people, the use of pesticides for pest control is not an ecological sin. When their use is approached from the sound base of ecological principles, chemical pesticides provide dependable and valuable tools for the biologist. Their use is indispensable to modern society.

BASIC PRINCIPLES OF THE INTEGRATED-CONTROL CONCEPT

CONSIDERATION OF THE ECOSYSTEM

The first principle of pest control, around which all other principles revolve, is consideration of the ecosystem. An ecosystem may be defined as an area that includes living organisms and nonliving substances interacting to produce an exchange of materials between the living and nonliving parts. This definition is so broad that it has been criticized as being vague, ineffective, and too all-inclusive to be really useful in ecology. Agricultural ecosystems are no less difficult to define satisfactorily, and the very breadth of the definition emphasizes the most basic point of insect control: successful programs that have any hope for providing solutions to problems rather than serving as temporary palliatives must consider pest populations as one component of complex environments.

The ecosystem is here considered to be a unit composed of the total complex of organisms, including the pest species, their competitors, other associates, and their food, shelter, hosts, and culture; weeds and other plants; soil and water and their management; the over-all conditioning environment; and the various agricultural, industrial, and recreational activities of man. Control of populations is a function of the ecosystem, and knowledge of the role of all the principal elements of the unit is essential to an understanding of population phenomena. The most effective system for controlling pests can be devised only after thorough knowledge has been gained of the principles underlying the fluctuations of populations that make up the ecosystem.

The limits of an ecosystem are usually vague. However, the area encompassed must be large enough that the important biotic components are included to the extent that their major activities fall within its limits. For practical purposes, it is what the problem makes it. For example, an agricultural ecosystem will usually include a group of fields, their margins, and certain other types of surrounding areas, such as woods, streams, and weedy, uncultivated areas. It should be considered as a part of a much larger ecosystem. Areas remotely removed from an agricultural ecosystem, considered in the narrow sense, may be important in contributing some biotic components of the restricted agricultural ecosystem. The coccinellid complex, for example, is highly mobile, and extensive movement occurs from crop to crop and area to area, sometimes to and from distant areas of hibernation.

Size, density, and variety of host plants in the ecosystem affect pest density. These are important factors in pest-management concepts, because they can be managed or manipulated to advantage in regulating pest-population density.

Although ecosystems are complex, there is no need to be overwhelmed by the difficulty of acquiring all the data necessary for developing the most sophisticated integrated-control techniques. Much progress can be made by using simple pest-management programs based on limited understanding of components of the ecosystem. Appropriate and successful beginnings can be made by regarding the ecosystem as a complex of overlapping subsystems, each of which, from the standpoint of pest control, can be analyzed separately, with attention concentrated on the key pest species.

The most important factors in the population dynamics of any pest can be determined rapidly by determining the life-cycle stage most responsible for increasing or decreasing numbers of the pest and then pinpointing the causative mortality factors within this stage. This approach is basically simple and can be applied by anyone who has done a simple regression analysis. It is biologically meaningful and provides a useful framework for the development of population models.

Successful application of pest-management systems demands that the types of pest species in each ecosystem be identified. This allows for the synthesis of the most effective control program and gives proper consideration to the differences in techniques that may be used for control of different types of pests.

There are two primary considerations in focusing attention on the pest. First, in any agricultural or forestry ecosystem there are seldom more than a few key pests, and often there is only one. Serious, perennially occurring, persistent pests that dominate control practices because their populations often remain above economic thresholds and thus require continuing applications of pesticides may be defined as key pests. Second, the kind of damage they cause or their abundance determines the status of key pests. The damage potential of the individual pest species is an important consideration. Low numbers of some pests can cause high damage, for example, vectors of plant and animal pathogens, and those, such as ticks, that secrete toxins producing paralysis. Also, key pests often attack the harvested unit of crops. With these, it may be necessary to begin control procedures at relatively low population levels. For example, tomatoes attacked by the tomato fruitworm, *Heliothis zea* (Boddie), may suffer little loss in yield. However, the presence of a single entry site destroys the marketability of the fruit. When the same pest attacks grain sorghum, it primarily reduces the quantity of grain harvested and affects grain quality very little. Thus, considerably higher levels of infestation by this pest can be tolerated in grain sorghum than in tomatoes. In general, pests that transmit pathogens and those that attack the harvested unit of crops impose unusually stringent requirements on a control program, in that populations must be suppressed and maintained at unusually low levels.

Occasional pests, in contrast to key pests, vary in importance. They create problems only in certain areas or during certain years. Such pests are usually under adequate biological or environmental control. However, disruptions or weaknesses in control occasionally occur, and these permit the pest to increase to economic levels. These occasional pests are especially suited to integrated pest-management techniques, and it is against such pests that a system of corrective as opposed to protective treatment has its greatest impact. Also, insect-resistant crop varieties or strains have great utility for control of pests of this category. It is with these pests that means of predicting the occasional occurrence of damaging populations assume special importance. Accurate predictions of their occurrence in numbers above economic levels allow for the application of control measures in a manner that will bring the regulatory factors back into dominance in the shortest possible time.

Potential pests cause no significant damage under current conditions. In attempts to control key and occasional pests, care must be taken not to alter conditions through injudicious use of chemicals or through cultural practices to an extent that would permit potential pests to realize their potential and become occasional or key pests.

Agricultural and forest ecosystems vary widely in degree of stability, complexity, and the size of the area occupied. Each of these factors has important effects on pest populations and consequently affects pest-management practices. The kinds of crops, agronomic practices, changes in land-use patterns, and weather are important elements of stability. All except weather are subject to modification and therefore may be manipulated to influence pest-management practices. Variation in stability is influenced also by the duration of the host life cycle and length of the growing season.

The constantly changing, dynamic nature of agricultural ecosystems results in equally dynamic changes in pests and the problems they pose. Even the values of control procedures change in time and space with such variables as biological understanding, development of technological capabilities, changing natural conditions, and differences in economic thresholds. Perhaps in no other country has the magnitude of such changes been as great or their impact manifested so quickly and documented so throughly as in Israel.

During 1950–1965, agricultural ecosystems in Israel changed from that typical of primitive homesteads to modern mechanized farming. Although the changes have been equally apparent for large numbers of species, lepidopterous pests of maize and other gramineous crops provide excellent illustrations. Before the development of large-scale irrigation projects, *Sorghum vulgare* Person was the main summer cereal, and *Zea mays* Linnaeus was grown in small gardens and at margins of melon fields, for human consumption only. Irrigation allowed farmers to handle large areas of crops, to produce them throughout the summer, and to introduce new crops. At present, 12 species and several varieties of gramineous crops are being produced for grain, fodder, pasture, or industrial uses.

In 1930 there were two lepidopterous pests of major importance on summer cereals in Israel: *Sesamia cretica* Ledyard and *Spodoptera exigua* (Hübner). Eight other species had been recorded from cereal crops but were not considered to be of economic importance. By 1963, drastic changes in pest status had occurred. *S. cretica* had become more important with the change in cultural conditions that permitted three generations per year to be produced instead of one. The status of *S. exigua* remained unchanged, as did that of three other species present in 1930. Three species of *Chilo* could no longer be found, but *Chilo agamemnon* Bleszynski, first recorded in northwest Negev in 1959, had become the most serious pest of cereal crops. A previously unimportant species of *Chilotraea* had become so abundant and serious a pest as to preclude the growing of rice in reclaimed areas of the Hula swamps. Three other potentially important pests new to the country had been introduced and were widely distributed.

The situation in Israel is probably unique with regard to the rapidity of change of the agricultural ecosystem. However, rapid change appears likely to become an increasingly common phenomenon throughout the world in response to the demands of a burgeoning population for food, feed, and fiber. The need for food is increasing to the point that vast uncultivated areas of the tropics and subtropics must now be planted to cereal grains, pulses, and oilseed crops. Many new and serious pest problems may be expected to develop in such areas.

Some interesting changes have occurred in the past and are now taking place in the United States. They illustrate how man may control some of his pests very effectively, although unknowingly, by changing patterns of agriculture forced by economic and social changes. For example, pests of indigo relinquished that status as soon as development of the synthetic coal-tar dyes resulted in the abandonment of indigo culture in the United States. On vast acreages once devoted to cotton culture in the southern United States, the crop is not grown today. The boll weevil, once the major insect pest of the area, no longer maintains that status there.

The potential of indigenous species to become pests of new crops, varieties, or strains that are introduced into new areas or regions deserves serious consideration. The idea should be discarded that species, strains, or varieties of crops agronomically desirable in one area of the world can be transplanted to another without the hazard of furnishing the "bridge" necessary for some previously unnoticed pest species to span the distance from anonymity to the status of major pest, e.g., the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), on potato. The experience of the Israelis in changing the pest status of a number of species by bringing irrigation, fertilizers, and new crops to the desert is well worth study.

UTILIZATION OF INDIGENOUS NATURAL CONTROL AGENTS

Relative scarcity rather than great abundance is characteristic of most arthropod species; but occasionally many and often a few species develop very high populations over some portions, but not all, of their range. Such species are exposed to important population-regulating factors. Data are rapidly accumulating to support two points: biotic control agents usually make up a major portion of environmental resistance to increases in insect numbers, and insects and related arthropods reach pest status most often as direct or indirect consequences of man's activities. Thus, it is important that full use be made of indigenous natural control agents.

One of the most widely known and successful examples of this approach to pest control is that with orchard pests in Nova Scotia. Control consisted chiefly in obtaining maximum benefit from natural control agents already established in the ecosystem; introduction of new species was avoided. A supplementary measure was to apply pesticides, but this was resorted to only when economic tolerance levels were threatened. Thus it was possible to take maximum advantage of environmental resistance.

Similar but somewhat less sophisticated systems for control of cotton insect and spider mite pest complexes have been operating successfully for decades in Arkansas and Louisiana in the southern United States, and in California in the western United States. Although wide differences in agricultural ecosystems exist between these areas, many elements of the problems are common. Both have a single key pest on cotton and multiple occasional and potential pest species. The key pest in the south is the boll weevil and in the west is lygus bugs. Destructive populations of the occasional and potential pest complexes develop as a result of chemical control measures invoked for control of the key species. In both areas, advantage is taken of the ability of the cotton plant to tolerate considerable amounts of apparent injury and to compensate for appreciable amounts of actual injury and still produce maximum yields. Thus, it is possible to delay applications of insecticides and often to reduce the number required during a season to the point that indigenous predators and parasites can prevent populations of the complex of potential and occasional pests from reaching economic tolerance levels. Such a system is aided considerably in the case of the boll weevil by high mortality in the overwintering population and susceptibility of larvae and pupae to the hot dry weather that often occurs during development of the first and second generations.

MAINTENANCE OF ECOSYSTEM COMPLEXITY

It is an accepted principle of ecology that complexity tends to exert stabilizing influences and simplicity tends to exert disruptive influences in the ecosystem. The tendency of populations of pests of crops grown in monocultures to oscillate widely in "boom-and-bust" cycles is well known and is in strong contrast to the characteristically more stable populations of pests associated with polycultures or natural communities. It would be highly desirable to work toward the development of complex polycultures as opposed to monocultures, from the standpoint of pest control. The interplanting of various species and varieties of crops in a complex polyculture may result in yields of total biomass equal to or even greater than that produced in monocultures. However, it remains to be seen whether systems can be devised that are of satisfactory efficiency for planting, cultivating, and harvesting such complex mixtures of crops. Here, too, the principle of economic thresholds must be observed. Much of man's success on earth stems from his success in simplifying agricultural ecosystems.

AVOIDANCE OF DISRUPTIVE ACTIONS

Since populations of insects and related arthropods most often increase to injurious levels as a result of man's activities, it is important that disruptive actions be identified and either avoided or minimized, when possible. Making use of the selective action of pesticides on predator–parasite–pest complexes is one way this may be achieved. Differential mortality may be obtained under field conditions by paying attention to methods of pesticide application, formulation, and dosage rates; timing; area of treatment; residual activity of the pesticides; habits of organisms involved; and innate physiological selectivity.

APPLICATION OF MINIMUM SELECTIVE HAZARDS

The principle of minimum selective hazard may be defined as the application of chemical control measures to pest populations in such a manner that target populations are kept just below economic-injury thresholds. By observation of this principle, the selection of resistant populations is avoided or delayed, the possibility of resurgence of treated populations is decreased, adverse effects on nontarget organisms and the amount of environmental contamination are reduced, and the cost of control is lowered.

Under the influence of ready availability of chemical insecticides of unprecedented effectiveness, the decade 1945–1955 was one in which a philosophy was developed to the highest of "eradicating" pests from the smallest (for example, one fruit tree or a small field), to the largest (major portions of 10 of the southern United States) of agricultural ecosystems by the application of broad-spectrum pesticides at maximum dosage rates. During the early years of experience with these potent toxicants, few biologists had the insight to anticipate any serious problems from their use. For the first time, weapons were available that were effective enough and cheap enough to be used widely with immediately obvious effects, and they were accepted and used enthusiastically. Little consideration was given to the rather strange phenomenon that there was no reduction in populations of most pest species with which the grower had to contend at the beginning of each new crop season, although larger and larger amounts of increasingly toxic materials were being used.

Failure of these highly effective new insecticides to bring about long-time reductions in pest populations has been elucidated by analysis of a mass of extremely detailed data on forest insects in Germany. The strategy of killing as many insects as possible whenever population density exceeds a certain level may not be the most advisable action. Insecticides used in this manner apparently elicit the sort of homeostatic mechanisms that force the pest to remain at high densities most of the time. Species that persist for long periods of geological time do so only if they are successful in evolving homeostatic mechanisms that allow them to adjust rapidly to catastrophes. Insects and related arthropods have been remarkably successful at making such adjustments. Insecticides are only the most recent of a long series of potent hazards with which insects have been able to deal successfully.

Seed-dressings especially illustrate the principle of minimum selective hazards. The rice water weevil, *Lissorhoptrus oryzophilus* Kuschel, is controlled in the United States by seed-dressings with aldrin at the rate of ¼ lb/100 lb of seed as well as by broadcast applications of the same insecticide at 2 lb/acre. Another pest of rice, the grape colaspis, *Colaspis flavida* (Say), is also controlled by seed-dressing with aldrin, but the rate has to be increased to ½ lb/100 lb of seed. Where the latter or both pests are present, approximately one fourth the amount of insecticide required to control the pests in broadcast applications is necessary; if only the rice water weevil is present, control may be obtained with about one eighth the amount.

Both of these rice pests have ecological features that also illustrate the necessity for considering the ecosystem. Seed treatment for control of rice water weevil loses its effectiveness in fields where high populations of weed hosts such as *Echinochloa* spp. are present. These weeds allow large numbers of rice water weevil larvae to develop in an untreated environment, from which they migrate to the roots of the rice plants. This emphasizes the necessity for practicing proper weed-control measures in order for a specific insect-control measure to be fully effective. The practice of seeding rice in flooded fields rather than drilling the seeds in dry soil is becoming an increasingly accepted agronomic practice. The grape colaspis is never a pest where seeding in flooded fields is practiced.

The use of systemic organophosphorus insecticides, such as phorate or disulfoton, as seed treatments for control of seedling pests of cotton provides an even more striking example of the principle of minimum selective hazards. Both materials, applied at rates as low as ¼ lb/100 lb of seed, provide satisfactory control of aphids, thrips, and spider mites in many areas of the southern United States for periods of approximately 1 month after plants emerge. The amount of toxicant applied per acre is almost infinitesimal, because seeding rates of cotton range from 10 to 15 lb/acre. There are obvious advantages of this method of application compared with that of at least two foliage applications, each consisting of 1 or 2 lb/acre of a chlorinated hydrocarbon insecticide. The seed-treatment method is rapidly supplanting foliage applications for control of aphids and thrips. Unlike broad-spectrum, relatively long-persistent chlorinated hydrocarbon insecticides applied broadcast to fields, seed treatments affect only the individuals of those species that feed on plants grown from treated seed.

It may not be valid to assume, as many have, that seed treatments do not affect populations of predators and parasites. The effects on populations of such desirable species may be quite drastic. There is little difference in destroying a population by exposure to the direct effects of contact with a toxic chemical and starving it by eliminating its prey with the chemical. For those species of predators or parasites that are sufficiently mobile to leave fields in which prey or hosts are absent or are present in numbers too few to support a population, starvation induced in this manner is probably of little consequence. However, populations of the less mobile predatory mites and spiders may be seriously affected. In any case, the over-all disruptive effect of seed treatments is far less than that of broadcast application of broad-spectrum insecticides.

The application of pesticides to restricted areas affords an opportunity for observing the minimum-selective-hazard principle. One of the most intriguing examples of this principle is described for the horn fly, *Haematobia irritans* (Linnaeus). The sexes of this pest have different resting sites on cattle. Males use the area around the ankles almost exclusively. By treating this area only, the proportion of males to females, and consequently the number of females inseminated, is drastically reduced, and control of the pest is obtained.

EXCLUSION FROM NEW AREAS

Most species occupy only a small portion of the territory suited to them, and, except for specific physical barriers, there is usually no obvious topographical–climatic restriction of their area of distribution. Much more attention should be directed at efforts to exclude pests from those areas that make up the vast territory suited to them but in which they do not presently occur. There is little difference in the strategy of war, whether it be man against man or man against pests. Basic strategy in human warfare is to prevent the enemy from occupying previously unoccupied areas and to deny him access to certain other requisites, for example, food. This is also prime strategy in pest control.

The history of invasion of the United States by pest species is well documented and shows that man has been generally unsuccessful in preventing pests from invading new territory. More than 100 important insect pests have succeeded in both invading and occupying parts of mainland United States since 1900. The numbers by successive 10-year periods are 24, 26, 24, 15, 7, and 8; and 4 since 1960. It is encouraging that the numbers have declined rather drastically since 1940. This is even more encouraging when the sharp decrease in numbers introduced is considered in the light of the revolution in transportation and the almost continuous involvement of the country in worldwide military operations that has occurred during this period. The decline is suggestive that the tactics employed have become considerably more effective than those used during the first four decades. However, it may be argued that the decline in numbers of successful invaders is the consequence of a decline in numbers of species that have the evolutionary resourcefulness to occupy new territory successfully after it has been invaded.

Allowing an average of almost two major pests per year to invade and occupy new territory during the last 65 years cannot be considered spectacularly successful. However, there is no way of measuring the success of efforts in this direction. The comparative ease with which most introduced species have extended their distribution once entry has been gained argues for change in both strategy and tactics. The spectacularly rapid expansion of the area of distribution of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), in mainland United States is a case in point.

Another case is the recent spread of the pink bollworm, *Pectinophora gossypiella* (Saunders), to previously uninfested areas of the western United States. Emergency measures, consisting of repetitive treatments of large areas with broad-spectrum insecticides, are under way to prevent further expansion of the distribution of this serious pest. The key word in such a course of action is “emergency.” The emergency occurred many years ago when the pink bollworm first invaded this country. Similarly, the emergency posed by the cereal leaf beetle, *Oulema melanopus* (Linnaeus), occurred when it first invaded Michigan, at least prior to 1959 when farmers began treating for its control, and not in 1962 when eradication measures were invoked. The greatest weakness of current strategy to prevent establishment and spread of invading species into new territory is the lag between the time of invasion and the initiation of eradicative or containment measures.

Experience gained in the United States during the last half century shows the desirability of diverting a modest percentage of the sums currently being expended on control programs to two new areas of endeavor: research to provide the ecological and biological bases on which more effective control programs can be constructed; and more efficient survey and detection procedures that will allow control measures of truly heroic proportions to be invoked as soon as a new pest invader has been discovered, rather than after large areas of the country have been occupied.

It also seems reasonable that research of substantial proportions be undertaken on a number of important or potentially important pests that have not yet succeeded in invading mainland United States. Mere provincial interest in insect and related pests is an indefensible position for biologists to take, anywhere in the world, in view of shrinking distances and increasing contacts between various countries, which have come about with improvements in transportation. Methods on a global basis, developed from sound ecological bases, to prevent pests from extending their present distribution, should have highest priority as being the most desirable and economical of all pest-management systems. Otherwise, man faces the certain consequence of comparatively rapid spread of many important pests to the limits of their ecological adaptability. The sort of international cooperation that has developed for control of stem rusts of wheat and other cereal grains provides a model for what could be done to prevent spread of arthropod pests. Approximately 150 scientists at 85 locations in 40 countries are involved in this program.

CROP ADAPTABILITY TO ECOSYSTEMS

Time and place of crop production are commonly accepted as being determined by the suitability of climate, soils, and seasons. Consideration should also be given to the feasibility of producing a crop profitably in the face of virtually certain damaging attack by insects. It is just as important to conduct pest surveys as it is to conduct soil surveys and make studies of water availability and the climate of an area before deciding whether to grow a crop in such an environment. This may be of very great importance in less developed and developing nations as programs aimed at expanding and intensifying agriculture are initiated and carried out. Realistic pest management demands the application of this principle.

Production of sweet corn for the fresh market in many coastal plains areas of the southern United States provides an excellent example. The fresh-corn market demands that the product be free of damage by lepidopterous larvae as well as other pests. Because of high infestation levels of the corn earworm, *Heliothis zea* (Boddie), the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), and the sugarcane borer, *Diatraea saccharalis* (Fabricius), in many areas bordering the Gulf of Mexico, and restrictions imposed by the necessity for producing a product free of excessive insecticide residues, corn free of damage from these pests cannot be produced economically by any currently available method. However, some progress has been made in areas where the corn earworm alone is involved, by using a combination of resistant hybrids and insecticide treatment. In such areas, varietal resistance provides the additional amount of control required for successful production of the crop. Realistic pest-management practices demand that the decision be made not to grow sweet corn for fresh market in the areas where all three species occur, on the same basis that a decision would be made not to grow the crop because of soil, water, or climatic limitations.

Need for adherence to the principle of crop adaptability to pest problems is also demonstrated by the necessity for producing seed potatoes for the United Kingdom in the north of Scotland, where aphid vectors of a virus are relatively rare and comparatively virus-free seed stocks can be produced.

The recent large increase in acreage of soybeans grown in the United States as a result of increased demands for oil and protein, and acreage controls on other crops, raises the question of adaptability of this crop to certain areas because of pest problems. An answer to the question is especially necessary in coastal areas where the crop faces the certainty of heavy insect infestations each year. In much of the northern two thirds of the United States, where soybeans traditionally have been produced, the crop is virtually free of attack by important insect pests. However, in many of the states bordering the Gulf of Mexico, growers are faced with the prospect of attempting to produce a crop profitably in the face of certain attack by a complex of more than 25 species. None of these insects is currently a key pest, but at least 10 of them are capable of assuming this status. There are imposing numbers of predators, parasites, and pathogens present. In addition, soybeans, like cotton, can tolerate appreciable amounts of apparent injury to foliage without effect on yield or quality of seed. These elements provide the bases for development of an effective, although crude, pest-management program. By taking maximum advantage of indigenous predators, parasites, and pathogens, and the capacity of the crop for tolerating considerable amounts of apparent injury without loss of yield or quality, use of selective insecticides can be restricted to applications required to control populations of pests that reach economic-injury thresholds. Meanwhile, research can be done to increase resistance, especially the tolerance component in soybean varieties, to as many pest species as possible, for example. Thus, it may be possible to produce the crop economically in such areas until more sophisticated pest-management systems can be developed. Otherwise, growers will be forced to abandon efforts to grow soybeans in many areas bordering the Gulf of Mexico, because the economics of production are such that an extensive chemical-control program cannot be sustained.

UTILIZATION OF ECONOMIC THRESHOLDS

A basic element in pest-management systems is the principle of economic thresholds. Before an attempt to discuss this principle, the term "pest" requires definition and some discussion against an ecological background. A pest is a living organism that occurs in numbers inconvenient to man. The term is without strict biological validity, because it relates only to human values of health, economics, comfort, and esthetics. Pest status is attained only when population densities that may cause significant reductions in yield or quality of crops and livestock are reached or when man's health or comfort is threatened.

An economic threshold in this context is usually defined as the level at which damage can no longer be tolerated and, therefore, the level at or before which it is desirable to initiate deliberate control activities. The definition probably should be amended to consider a more critical threshold density as that where the loss caused by a pest just equals in value the cost of available control measures. It should also take into account any known adverse side effects, which may have ecological consequences that cost more in values lost than is gained by control of the pest in question. Examples of this are the use of insecticides that reduce biotic control agents to the point where they are no longer effective and are not likely to become so again for some time, or the use of persistent insecticides that leave residues in soil which prevent the growing of succeeding crops on the treated areas because of the possibility of excessive residues occurring in the produce, e.g., soybeans following corn on soils treated with aldrin or heptachlor for control of soil insects. The amended definition takes into consideration the dynamic nature of the pest problem and allows for the establishment of relative criteria of injuriousness measured according to the general level of the economy in space and time. The determination of these thresholds is prerequisite to the development of any system of pest management for two main reasons: first, the level of pest populations below which damage is tolerable must be known, thus defining the ultimate objective of the control system; second, the level must be known above which new emergency elements of the integrated program must be applied or invoked to avert significant injury and an outbreak of the pest organism.

To obtain this information, a clear picture of the complex economic factors associated with the production of the crop of interest is vital. First, the general economic picture must be known, and what might be called the economic degrees of freedom must then be determined. In other words, the margin of profit on which the agriculturalist or forester is operating must be determined so that the amount he can afford to lose to the depredations of pests can be assessed. Second, and against this background, how much can be afforded for protection against this level of loss must be established. For example, if a grower can afford to lose *X* hundreds of dollars per acre to pests and still show a reasonable profit, he can afford up to but not more than *X* hundreds of dollars for protection of his crop by use of the control methods available to him. If his crop can be protected for less than this amount, the difference will be added to his profit. This knowledge defines the problems more clearly and sets the limits on the cost and value of the management systems that can be developed. See Chapter 18 for further discussion of the economics of pest control.

It is difficult to determine economic thresholds and levels of tolerance because of the great number of factors involved and because many of the factors are economic and not readily available to or assessable by animal and plant scientists. It is axiomatic that the threshold levels will change constantly with changing economic and environmental conditions; they themselves are dynamic, and this adds weight to the arguments in favor of multifaceted, flexible control systems.

There have been few analyses of the economics of crop production relative to pest problems, and principles have rarely been developed or limits clearly defined. Consequently, it is not unusual for more to be spent to control a pest than the value of the commodity the pest could destroy, or, even worse, for helpful insects to be destroyed at considerable cost. Moreover, the application of a pesticide to destroy pest *A* may upset balances to such an extent that new pests, *B* and *C*, are created, which in turn require still more money to control. This sort of synergism strains the boundaries of even the most liberal margin of profit and yet can only be clearly exposed by a detailed analysis of the economics of crop production in relation to pest control.

On the basis of the available fragmentary evidence, it may be concluded that economic threshold levels are almost invariably higher than expected. Too frequently, the visual threshold, the population level at which individuals of the pest species are obvious, is synonymous with the action threshold, and both are equated with the economic threshold. The action threshold is the level of pest population at which action must be taken to prevent the population from rising to the economic threshold where significant damage occurs. Ideally, it would be desirable to have control systems that are so effective and self-perpetuating that the necessity for action is avoided. Most systems, however, will probably require periodic action; thus the determination of the action and economic thresholds becomes of supreme importance.

The level of economic injury is difficult to determine. This is often assumed to be the level at which significant number of pests destroy important quantities of product, but in most cases it is a subjective determination. Damage that causes nutritive loss or adversely affects the usability or palatability of the product is far more important than damage that merely affects appearance. Esthetic values may easily be overemphasized in this regard, and modern marketing and sales promotion tend to encourage this error. The harmful effects of even quite notorious pests have proved to be remarkably difficult to document, and the very natural assumption that if a pest destroys a fruit or feeds on a tree it is causing economic injury is not always supported by the facts. It is even more difficult to determine the economic thresholds of most pests on most crops.

PREDICTION OF POPULATION TRENDS

Once the economic status of the pests occurring in an ecosystem has been determined, studies on the biology and ecology of the pests must be developed. These have two purposes: prediction and manipulation. The main value of being able to predict future trends in the population levels of pests is that it enables the intelligent application of control measures to prevent rises above the economic-injury level. Most pest-management programs will be complex interwoven systems with a number of major components. Pest populations will certainly not be eliminated in these programs but, rather, will fluctuate at low levels generally acceptable to man. From time to time these fluctuations will approach the economic-injury level. If reaction to such fluctuation is in the application of vigorous extra measures, the system may be permanently disrupted. Therefore, means for predicting future population trends with accuracy and confidence must be developed, so that new components may be added to the system only when required to damp potential outbreaks; in this regard components must be selected that have a minimal disruptive influence on the system as a whole. When danger is past, these components should be dropped from the system until they are again required. This kind of prediction is particularly important after a satisfactory system has been developed—in the operational phase of the study.

Manipulation is also basic to the establishment of such systems. The factors is an agricultural ecosystem that affect pest numbers, or that have the potential to do so, must be determined, and those with the greatest utility must be selected and so manipulated that their regulative effect in the ecosystem as a whole will be maximized. When this has been done and the most value is being obtained from natural factors of the ecosystem, it may be found that the pest populations of interest are reduced to tolerable levels without further action. If not, means of adding new components to the ecosystem may be considered; these components will complement those already present to produce the required levels of pest abundance. In the rational and organized development of pest-management systems, this step-wise progression in research, from determining important environmental factors, through manipulation to maximize their effectiveness, to the addition of supplemental components, is essential.

MAINTENANCE OF SUBECONOMIC POPULATIONS

Full development of integrated control systems requires the continued existence of pest populations in the ecosystem. This is the most difficult aspect of the integrated-control concept for many to grasp. Low pest densities may need to be conserved to maintain the pest-management system and to provide the necessary elements of permanence and dynamism. If the pest is completely eliminated, many of the regulating components of the ecosystem also may disappear. Pest-management systems often cannot operate without the presence of pests in subeconomic populations. In the absence of these critical components, the pest-management system can no longer function as a self-generating system if the pest reinvades the ecosystem, as it is almost certain to do. The subeconomic pest population and its associated natural controls need not always be in the crop-growing area. With highly agile populations, they often are not but may be in associated uncultivated areas, hedgerows, weeds, and cover crops.

Pest populations can be tolerated at levels that have no effect on crop yield and quality. The mere presence of an insect pest is not a threat of economic damage, and pests do not have to be eradicated to be controlled.

SUCCESSFUL UNILATERAL PEST-MANAGEMENT SYSTEMS

Systems of pest management based on the single-factor approach are proving to be less and less reliable. Nevertheless, there are examples in many unilateral systems that have worked successfully for decades and show no evidence of declining in effectiveness. All such examples show evidence of having been developed from intimate knowledge of biological and ecological principles. The various approaches have been based on manipulation of ecological niches, with the objective of disrupting ecological requirements or of augmenting ecological intolerances.

Biotic requirements such as food, breeding sites, and shelter are vulnerable requisites for pest species. Denying access to one or more of these is an enlightened ecological approach that has been demonstrated to be effective. Two of the most successful demonstrations of the approach have been the complete control of the grape phylloxera in the vineyards of Europe by use of American grape rootstocks on which the insect cannot complete its life cycle, and control of the Hessian fly, *Mayetiola destructor* (Say), in many areas by use of varietal resistance in wheat.

Satisfactory control of the southern cattle tick, *Boophilus microplus*, (Canestrini), on cattle in Queensland has been obtained by denying the pests access to their hosts for periods long enough to break the life cycle. This technique of pasture "spelling" was based on data showing that ticks detaching from their hosts during mid-April to mid-July produced few or no progeny. The reasoning that formed the basis for the approach was that if cattle were moved to an uninfested or sufficiently lightly infested pasture in May and kept there until larvae in the alternate pasture died, the life cycle would be broken, and that moving cattle at 4-month intervals thereafter would prevent any small residual infestations from increasing to troublesome levels.

An example of excluding a pest from its host by temporal separation of the two is provided by a system used for control of the pickleworm, *Diaphania nitidalis* (Stoll). Cucumber can be profitably grown as either a spring or fall crop in much of the temporary range of the pickleworm. The method takes advantage of this fact plus detailed knowledge of the biology of the pest, which is endemic in areas bordering the Gulf of Mexico. The insect disperses northward each year, extending its range with each generation until it is eliminated from its temporary range by cold weather. It is successfully controlled by producing pickling cucumbers as a spring crop, before the annual invasion of the pest, thus avoiding infestations.

Control of a pest complex has been obtained in Egypt simply by changing the planting date of maize, *Zea mays* Linnaeus. Prior to development of this method, maize was planted throughout April to September, and the stem borer complex–*Ostrinia nubilalis* (Hübner), *Sesamia cretica* Ledyard, and *Chilo agamemnon* Bleszynski–caused such severe damage to the crop that growers had to resort to extensive application of insecticides for control. By confining the planting dates to mid-May through mid-June, excellent control of all species has been obtained, and yields have increased substantially.

FROM CHEMICAL TO INTEGRATED CONTROL PROGRAMS

It is too often assumed that once a unilateral pest-control program based on multiple applications of broad-spectrum insecticides has been adopted it is impossible to revert to an integrated control program. It may be true that when such a program fails and a multifaceted pest-management system has to be substituted there is likely to be a difficult period of transition. During this time the grower may have to be willing to sustain a considerable amount of damage until corrective measures have operated long enough to allow the necessary factors to become effective in the ecosystem. Such transitions can be made successfully, as illustrated by the well-known work on orchard pests in Nova Scotia, the spotted alfalfa aphid investigations in California, and the less publicized but equally impressive studies on cotton pests in Peru.

In Peru, cottongrowers of the Canete Valley were forced to abandon the single-component system of complete reliance on application of broad-spectrum insecticides because of the development of insect resistance to insecticides, resurgence of treated populations, and elevation to pest status of several species of minor or no previous importance. Reasonably complete records for more than 30 years are available to chronicle the history of pest control on cotton in this narrow, isolated valley.

Prior to 1939, only six species were considered to be pests in Peru, and they were controlled by the use of arsenical and nicotine insecticides and hand picking of insects and infested fruit. These methods allowed a high degree of natural control to be exerted by indigenous predators and parasites. By the 1949–1950 crop year, virtually complete reliance had been placed on the applications of large amounts of broad-spectrum insecticides, such as DDT, benzene hexachloride, and toxaphene, or mixtures of these with sulfur. The most important pests were the tobacco budworm, *Heliothis virescens* (Fabricius), and the cotton aphid.

Results of the new program were good during the first 5 years. Good control of the pests was obtained with consequent increases in yields. However, after the third year it was observed that the insecticides were losing their former effectiveness. New insecticides, such as aldrin, dieldrin, and endrin, and various mixtures of these, were used, and intervals between applications were reduced. This increased costs and failed to improve the situation in many cases, and growers changed to the use of organophosphorus insecticides, such as parathion and mixtures of ethyl and methyl parathion.

After these insecticides were used for a few years, six new and important pests appeared. The situation deteriorated rapidly as several of the pests developed levels of insecticide resistance bordering on immunity, and it culminated in 1956 with the worst crop in the history of cotton production in the Canete Valley. Nearly 50% of the crop was lost after an average of 12 applications of insecticides failed to give adequate control of the pest complex.

Based on experience to this point, both growers and experiment station personnel concluded that it was not possible to continue profitable cotton production based on chemical pest-control programs, and in 1957 a pest-management system was adopted that contained elements of chemical, cultural, biological, and regulatory methods. The system was based on the following key points: (1) reduction in the planting of ratoon cotton (crop produced from plants cut back and allowed to produce new growth from the crown) to less than 25% of the total area; (2) preparation of soil without irrigation to obtain increased destruction of *Heliothis virescens* pupae; (3) repopulation of predators and parasites by introduction from other valleys or foreign countries, or by artificial rearing for release; (4) establishment of mandatory planting and crop-residue destruction dates; (5) adoption of recommended irrigation schedules; (6) adherence to the various cultural methods considered to be sound agronomic practice for production of uniformly early crops; and (7) limiting insecticides used to arsenical and botanical materials only, except under very special circumstances, which allowed application of systemic insecticides at dosage rates one fourth to one half of that recommended by the manufacturer to control *Aphis gossypii.*

Seven years after the initiation of this program, apparently the insect problems have been solved and the natural balance between detrimental and useful insects has been restored. More than 30 species of predators and parasites are currently playing an important role in control of the pest complex. Finally, yields have increased by about one third compared with the 1950–1955 period, when control was based on the exclusive use of insecticides.

DEVELOPMENT OF INTEGRATED SYSTEMS

The purpose of this section is to describe the information required for the development of integrated pest-management systems, to explain how this information may be obtained, and, finally, to discuss the ways in which it can be used to design such systems.

The problem of building an integrated control program by organized, deliberate effort is essentially one of systems design. The problem of obtaining the information that will furnish the building blocks for this design is largely one of analyzing various systems. Researchers have taken a remarkably unsophisticated approach to these problems, an approach highly colored by traditional training and experience as applied biologists and largely ignoring the development of tools with tremendous potential value by theoretical biologists and biomathematicians. This fault is not entirely one-sided. If traditionalists could learn to become more mathematical and theoretical, and if the new school could become more biological, an effective collaboration could develop, with potentially great revolutionary consequences.

Living organisms are multicomponent open-chain systems that combine remarkable stability with great sensitivity to change. Such systems are difficult to describe, let alone analyze, and yet they must be analyzed if pest-management systems are to have a rational and firm basis in fact and understanding. Without mathematics it is hardly possible to think about entities with more than two or three variables, and yet there may be thousands of variables in a biological system. The problem is to select those that must be studied and to determine how few of them are adquate to explain the system's behavior.

Many ecologists object to this approach, protesting that ecosystems and population processes are too compex to allow hope for detailed and precise analyses. However, there is little in physics and chemistry to rival the striking success and broad sweep of genetic theory. It stands as a rebuttal to those who maintain that biological phenomena are too complex to yield to theoretical analysis. Applied ecologists must either equip themselves for such analyses or interest the theoreticians in the problems. The importance of agricultural and forest industries to over-all economic well-being fully justifies this attention, but the ultimate applied nature of the problem may repel the theoretician.

Systems theory is a special kind of formal approach to biological problems. It is based on the modern development of information theory, game theory, operations research or cybernetics, and computer development. Everyone is familiar with the notion that the whole is greater than the sum of its parts. The concept of systems and systems theory is closely tied to this idea. In other words, a system of interacting entities has certain properties that are not obvious properties of the component entities themselves. The primary problem in studying such entities has been to predict the properties of the whole from the rules of interaction between its components. The type of question posed is how the properties of a biological system are the result of their being a complex array of interacting elements. Homeostatic problems have been the core of much of the biological work on systems theories; these also lie at the heart of understanding population phenomena.

In formal treatments of organizations, such as an ecosystem, much use is made of a simple conceptual device called the black box. This name is used for an object about which the following is known: it can sense a certain repertory of inputs, generates a certain repertory of outputs, and associates outputs to inputs according to a certain repertory of admissible laws. The black box can represent anything desired, for example, a particular behavioral feature of an organism, such as predation. If the jargon is stripped from the above statement, what emerges is that predacious behavior (output) is a response to certain environmental factors, both internal and external (input), and that its expression falls within certain limits (the laws).

The black-box concept had its origin in systems engineering. In the design of a complicated system, it is difficult to consider all parts at the same time. Therefore, an attempt is made to separate the function of the entire system into independent component functions, each of which is represented by a black box. When this has been done, separate consideration can be given to the problem of how to replace each black box by some real object or activity that will yield the desired function. This describes exactly the problem of designing integrated control systems and presents a new, simple, and refreshing view of a way in which it can be approached.

Detailed information on many components of the ecosystems in which pests operate is essential to the design of integrated control systems, and obtaining this information can be viewed not only as a problem in ecology, but also as one in systems analysis. The black-box concept is also useful in the analysis of systems. In studying any particular function of a living system, it is not necessary to analyze the nature of every single factor involved; some factors can be replaced by black boxes, and the analytical effort can be concentrated on one or a few factors. In either context, the black box is merely a symbolic representation of functions associated with a given object or class of events. The progress of both systems design and analysis can be symbolically represented by a progressive replacement of black boxes by white boxes. A white box is a system of known components put together in a known fashion to produce a given result. The replacement of every black box by a white box is a possible solution of the task. Although the contents, or properties, of a black box are not known, the usual purpose of isolating it as a unit is to discover or hypothesize what they are. To do this, the black box is tentatively replaced in the over-all system by a white box whose contents are known and have deliberately been chosen so that the input–output relations of the white box will be the same as those observed for the black box it represents. The white box, therefore, is a model, hypothesis, or explanation of how the black box works.

There are several principal mathematical theories of systems, such as cybernetics, game theory, and communication theory. Cybernetic analysis has merits that are particularly revelant to a consideration of integrated control systems; one is the way in which it permits the partition of systems design and analysis into clearly separated components, or black boxes, for specific study. Another is that it recognizes the general importance of feedback, or the guidance of control actions through sensing or monitoring their results.

Game theory deals with situations of conflict between two or more objects or procedures. Input and output repertories difficult to specify in natural situations are replaced by a repertory of well-defined possible moves. The mathematically difficult problem is that of generating the strategy, or the law that prescribes a move for every possible situation. The basic rule is to design a strategy such that the expected gain is maximized (for example, crop yield) if the opponent (pest) follows what for him is an optional strategy (perhaps reproduction, feeding, or movement). This is what is being attempted in designing integrated control systems, but the methods are empirical and imperfect; they are based more on natural history and descriptive ecology than on theoretical biology. The advantages of placing efforts on a sounder basis of theory and of taking advantage of the techniques of systems analysis and design are obvious.

The claim will be made that the approach is too sophisticated for an essentially field-oriented applied problem. If the theories of systems analysis and design were adopted by applied ecologists concerned with pest control, they could be adapted to meet specific aims. This would require basic research in biomathematics and theoretical biology, but once adapted as a routine tool to be used for integrated control systems, shortcuts and simplifications would undoubtedly follow that would place the tool within the reach and comprehension of all.

Systems analysis and design have already been used to advantage in problems of fisheries and wildlife management. Moreover, some entomologists are using systems analysis in studying population processes, such as predation and attack, that are of direct and significant interest to those using predators or parasites as a biological control component of pest-management systems. Other ecologists are attempting, on a purely logical basis, to study problems of pest control by separating the biological systems of concern into their component parts, or black boxes. They could benefit greatly by adopting not only the logical basis of systems analysis and design but also the methods of mathematics that are already available for this approach.

There are many advantages in opening the doors of a narrow, problem-oriented research world to the strengths that have been developed elsewhere. Some of these are: Approaching research on incredibly complicated population phenomena through systems theory would bring order, organization, and coherence to efforts expended; the information necessary for pest-management systems could be more clearly defined, and data for use in designing such systems could be processed more efficiently; encouraging the analysis of individual components would lead to simplicity rather than what has been called a "sea of confused complexity"; advantage could be taken of the principles of systems analysis and design already developed, but largely unknown to applied ecologists; advantage could also be taken of the mathematics for handling systems that are now available and being actively developed; and, finally, computer programs for systems analysis and design are already available that could be adapted to the problems.

With this background, and bearing the theories of systems analysis and design in mind, consideration is given to the information required for the perfection of pest-management systems. This is a matter with two distinct aspects: the analyses of the ecosystems with pest problems that will provide the needed information; and the ways in which this information will be used to design control systems.

The major difficulty in determining which factors in an ecosystem regulate pest populations, or have the potential to do so, is that of gathering the complex data required and of analyzing them to extract the required information. One particularly useful tool, the life table, is now available. This can be a highly sophisticated research device or a relatively simple tool, depending on the orientation and interests of the research worker using it. In the development of pest-management systems, a simple form of the life table will probably meet the needs satisfactorily. This can be thought of as a profit and loss analysis of the dynamics of the pests, with the determination of the causes of major losses, or mortality. Analyzing the dynamics of any organism to determine the most important factors can be done simply by determining the life-cycle stage most responsible for increasing or decreasing numbers and then pinpointing the causative factors within this stage. Percentage of mortality is not good measure of the importance of a factor affecting the dynamics of a pest; variation is the important attribute of mortality, and low but variable mortality may have considerably more importance than high but consistent mortality.

It is difficult to believe that satisfactory control systems can be developed rationally without an understanding of the dynamics of the pests of major concern. As stated previously, such a foundation permits maximum value to be taken of factors already operating in the ecosystem to cause mortality to the pest, and then, but only then, to add new factors as required.

Successful pest-management systems will probably have many components, and research in many areas will be pertinent to their evolution, with varying degrees of directness: toxicology, plant resistance, genetics, and almost any field of biology that can be conceived. Certain related research fields, however, are of paramount importance to the perfection of management systems: (1) bioclimatology, because without an understanding of the ways in which weather affects population levels and trends, prediction is impossible; (2) toxicology and studies of the effects of different kinds of pesticides on both harmful and beneficial insect species, better understanding of the mechanisms of resistance to insecticides, and ways of managing populations to avoid or delay the development of resistance, because, without this information, pesticides that will affect the pests in desirable ways and yet have minimal effects on beneficial species cannot be incorporated; (3) studies of the principles of parasitism and predation, because without knowledge of these principles it will not be possible to put the selection of beneficial species for inclusion in the system on a rational basis; and (4) studies of the effects of host-plant resistance on populations of predators and parasites and the effectiveness of pesticides.

The need for knowledge has so far been explained on the basis of economic relations between pest populations and crop production, and the requirement for information on the dynamics of pest populations so that existing factors can be manipulated and thus have their maximum influence, and so that new factors can be introduced to the system to complete the process of regulating densities at acceptable and satisfactory levels. One of the most difficult problems must now be considered: selecting the components to be added to the system and ensuring harmony among those selected with the entire ecosystem background. It must be ensured that the components of the management program are fully compatible, perhaps even synergistic, and do not disrupt or interfere with one another. This is essentially a problem in optimization, and much can be learned of this from advances made in other fields, such as fisheries and wildlife management. The only major differences between these fields and entomology is that they are concerned with maximizing animal populations as the harvestable commodity, whereas entomologists are interested in maximizing livestock and crop production at the expense of pest populations. The principles are the same.

When thought about in terms of devising systems for the entire array of pests in a crop ecosystem, enormous complexity is being added to the problem of harmonizing the components of the system. Actually, any specialist in computer technology can help find the solution of this problem of complex, multivariate systems, but entomologists have not yet fully realized this great potential. Computer games such as simple numerical routines that mimic the effects of environmental factors to simulate pest populations without control and with a variety of insecticidal applications, or dynamic programming, a computer device involving multistage decision processes, could be used to determine optimal control strategies. These exercises in the game-theory aspect of systems design have value for synthesizing real management programs. All that is needed to realize this value are data collected from actual field situations. These can be supplied through research.

A number of theoretical considerations indicate that the integration of two or more techniques into a unified pest-management system should provide more effective and less costly control of most pests, and pest complexes, than the use of any one method alone. It has been generally accepted, for example, that the use of conventional insecticides is highly efficient in terms of numbers of insects destroyed at high population densities but is relatively inefficient when populations are low. Conversely, release of sterile insects is inefficient at high-population and efficient at low-population densities. Integration of the two methods should provide a system of pest management much more efficient than either used alone, especially if the sterile-insect release component should provide a means of reversing the law of diminishing returns, as has been postulated, that operates in all unilateral systems.

In an area occupied by a pest, the cost of attaining any given level of control by an agent that actively seeks the pest will be proportional to the total population and largely independent of area, while the cost of a passive agent that does not seek the pest will be proportional to area and independent of the population. For example, if an insecticide gives 90% control of a pest population, it would be expected to do so whether the pest density was 1 or

100 per unit area, and the cost would be the same. The same result would be expected from the application of pathogens, field treatment with chemosterilants, or the use of attractants or traps.

The cost of rearing the number of parasites, predators, or sterile males required to attain any given reduction in a pest population will be proportional to the size of the population. Only the cost of distribution, generally a small part of the total, will be partially dependent on area. Therefore, passive agents are likely to be cheapest when pest densities are high, and active agents should be less expensive at low levels. Suppose, for example, that pest density averages 10,000 insects per acre, with a rate of increase of five times per generation. Suppose that the economic threshold is 2,000, that an insecticide application giving 80% control costs $8 per acre, and that one application per generation will be required to hold the population as the economic threshold. Now suppose that parasites cost $2 per thousand and that each parasite destroys one host if enough are released to give 80% control. That would be 8,000 parasites costing $16 per generation, or twice the cost of insecticides. However, suppose that an insecticide was first used to reduce the population to 2,000, then this was followed in the same generation with the release of parasites to reduce it another 80% to 400 hosts. The parasites would cost $1.60. In the first generation, then, the cost would be $8 + $1.60 = $9.60, but the continuing cost of holding the population at the 400 level would be only $1.60 per generation, as against $8 for insecticides alone or $16 for parasites alone at the higher mean population.

Still another theoretical advantage of multifaceted pest-management systems results from the law of diminishing returns, which applies to all methods. If the intensity of any agent is increased to achieve a higher kill, there is a point beyond which the dose or the work required will increase exponentially as control increases, and the efficiency per unit of cost will decrease proportionately. For instance, the quantity of an insecticide required to kill insects increases exponentially as the percentage of control increases. In one experiment in which schradan was applied to the corn planthopper, *Peregrinus maidis* (Ashmead), a concentration of 1.5 mg/ml of solution killed 50% but 6.25 mg/ml, or more than 3.5 times as much material, was required to kill 100%.

The same rule holds for the release of sterile males. Theoretical calculations, well supported by experimental data, show that to increase control from 30 to 60 and 90% would require an increase of 3.57 times and 21.42 times in the numbers of sterile males released instead of 2 and 3 times, as might be expected.

Many laboratory and some field experiments show that the exponential rule also applies to the release of parasites or predators. Thus, in Canada, pupae of the European pine sawfly *Neodiprion sertifer* (Geoffroy), were placed on a lawn in the open, and varying numbers of the parasite *Dahlbominus fuscipennis* (Zetterstedt) were released. The control was 11.3% with 25 parasites, 19.0% with 50, and 40.1% with 200. When workers in Poland released *Trichogramma* against the plum moth in orchards, the control was 81.5% with 2,000 parasites per tree but only 91.3% with 20,000.

The rule of exponential increase in cost means that it will often be cheaper to use two methods in sequence instead of one alone. Whether or not there will be a saving, and the amount, will partly depend on the cost of the methods used. Obviously, two methods will not be cheaper than one if one of them is very expensive. The saving will also be influenced by the proportions of the total cost that can be charged to materials or application. For example, doubling the degree of control might take 4 times as much insecticide, but it would cost no more to apply it. Application of computer technology can greatly improve the efficiency of experiments designed to study problems of this sort under actual field conditions.

In summation, there are three clearly defined primary research needs for the development of integrated pest-management systems. First, research is needed on the economics of crop production relative to pests and pest control, and on economic injury levels relative to individual pest species. This is to clarify the importance of the pest problem so that the required intensity of population regulation can be defined. Second, analysis of the dynamics of the pest populations relative to mortality factors already operating in the ecosystem is necessary to provide the information required to predict future population trends and to enable the most effective factors to be intensified through modifications or manipulations of the environment. Third, supplemental methods of control available for use in the particular ecosystem of interest must be evaluated to determine which are most suitable for the needs, and to harmonize these into the existing system to produce optimal crop production relative to pest infestations.

The pests against which the successful management system is developed, as well as other components of the ecosystem, are dynamic. Therefore, the management system itself must be dynamic and have great flexibility. This means that when an integrated program has been developed and applied, it must not be expected that the job has been finished; continual changes in its details will be needed to adapt it to the dynamic ecosystem. New components must be added and former ones removed as their usefulness passes. To maintain this flexibility, there will have to be frequent monitoring of the major components of the ecosystem. This is not primarily a research activity, but rather maintenance most suitably accomplished by extension personnel or by sophisticated growers themselves. It will be based on the research date of the developmental phase but will not itself require great precision and detail. If background data are adequate, shortcuts to sampling and analysis can be taken. This operational phase might require as little as merely making periodic visual assessments of a control system or as much as regular sampling or trapping to follow population changes.

The research worker required to meet the needs of this rapidly evolving philosophy of pest control will be an entomologist trained for research on pest-management systems—one who is first and foremost a biologist in the broadest sense, one with a good background in traditional entomological principles, but also fully familiar with behavior, toxicology, population ecology and genetics, resource management and the techniques on which it rests, systems analysis, economics, biomathematics, and computer programming. Above all, he must have a personal outlook highly colored by flexibility, imagination, and receptiveness to new ideas. Such a person would indeed be a paragon, and the only practical way in which this array of talents can be brought to bear on the complex problems of pest control is by the formation of teams. Cooperative, interdisciplinary research and the team approach are becoming as essential to the evolution of pest-management systems as is the meeting of these research needs.

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CHAPTER 18

Economic Principles of Pest Management

Economics is the study of the allocation of scarce resources among competing ends. Resources can be classified as land, labor, capital, and management. Economists attempt to determine the optimum allocation of these resources among the competing ends for the consumer, the business firm, and society as a whole. Because of the diverse nature of economic problems related to insect control, several fields of economics need to be drawn on for a thorough analysis. Microeconomics is employed to deal with problems relating to the individual firm, consumer, and resource owner. Aggregative economics is used in determining the effect on the productivity, location, and organization of agricultural production. Welfare economics deals with the evaluation of alternative public policies. Analyses in welfare economics are generally oriented to economic welfare and do not include other social decision-making criteria.

Entomologists develop and perfect various methods of insect control and determine their physiological impact on agricultural crops, forests, livestock, and human beings. Economists depend on entomologists, biological scientists, and physical scientists for information on the nature of the relationships among the various inputs that are combined to produce a particular product. Values are attached to the inputs and the product produced under alternative insect-control systems, and these make it possible to select the pest-management program that is best in terms of cost and returns.

Because most of the insect-control decisions presently available to farmers involve the use of chemicals, most economic decisions of a farm firm regarding pest control are primarily concerned with chemical control methods. The use of biological controls generally involves a larger decision-making unit than the individual farmer. Decisions regarding insect sterilization and biological control measures must be made on an area basis. The areas range from small local areas to multicountry areas.

ECONOMIC RESEARCH ON INSECT-PEST MANAGEMENT

Economic research on insect control is concerned with providing answers to problems related to the costs and benefits associated with various insect-control methods. Economists evaluate pertinent cost and benefit factors to provide information useful to decision makers involved in the production and use of pesticides. A comprehensive economic analysis should include all major decision makers and decision-making areas. However, to limit the analysis to manageable proportions, it is generally necessary to consider only the most important aspects of the problem and assume that the rest of the factors have a negligible effect.

There are at least three major sets of decision makers who need information related to the economic consequences of the various insect-control systems. Their decisions and actions determine the type and amount of each insect-control system that will be used. They are the farmers, the industry providing the insect-control systems, and governmental or other public agencies. Because the primary objectives of these units are different, the type of economic information required is quite varied; thus, the type of economic analysis employed to obtain this information will also be quite varied.

First, the producer must decide whether or not to use any insect controls. Such things as costs and returns, risk and uncertainty, and convenience are usually primary factors entering into the decision. If some method of insect control is considered necessary, he must then decide which of the available controls will be used, when to use the control, how frequently the control will be used, and how much control to use.

Industry makes decisions on the chemical or biological products to be produced, research to be undertaken, territories and outlets to be served, prices to be charged, promotion to be given, and services to be offered.

Government employees make decisions related to the general welfare of individual segments of our society and to society as a whole. They decide how their funds will be spent for public research and education needed to provide effective insect-pest management and control. They also decide whether insect-control measures may be used for specified purposes and the ways in which they may be used.

The information included in this chapter applies to the three sets of decision makers. However, the proposed methodology and examples used emphasize the economic principles most useful for evaluating alternative methods of pest management on the farm.

ECONOMICS OF INSECT CONTROL ON THE FARM

Insect-control systems affect the productivity of agricultural and forest crops. They allow producers to specialize in a particular crop and also permit concentration of production in a favorable area.

A major concern of the farmer is, "Will it pay to use this method of insect control?" The answer to this involves examining the costs and returns directly associated with the use of the insect-control method whether chemical or biological, as well as the effects on the rest of the organizational unit. While this discussion deals with a single farm as the unit faced with the decision, the analysis could also be applied to other organizational units.

In economic analyses, profit maximization is most often considered to be the primary goal, or at least the most measurable goal, of the individual farmer. There are several additional factors that may influence the farmer's method of operation. Such things as desire for more leisure time, ease of handling, and safety of the insect-control methods may temper the farmer's goal of maximum profit. Therefore, it can be assumed that profit maximization is attempted within the constraints set by the farmer. Maximization of profit occurs, subject to his limited resources, when the following three conditions are met: (1) The resources involved in the production of a single product should be combined so that the marginal returns from the last dollar invested in each resource are equal. For example, in producing cotton, returns from the final dollar spent for insect control should be equal to returns from the final dollar spent for fertilizer, labor, and other resource inputs used in producing cotton. (2) When producing more than one product, the marginal return per dollar invested in a resource should be equal in all its alternative uses. For example, the return for the final dollar spent for insect control on cotton should equal the return for the final dollar spent for insect control on all other crops. (3) If resources are not restricted in quantity, their use should be increased as long as the added cost of obtaining an additional unit of product is less than the added value of that product. For example, more insecticide should be added as long as the added cost of the insect control is less than the added value of the additional crop resulting from the added increment of insecticide.

Certain key factors need to be examined by the farmer faced with the question of whether it will pay him to use a specific control system. These are factors relating to the effects of the control systems on input–output relationships, costs and returns, and risk and uncertainty. It is important to know the magnitudes of input–output relationships, because they have a direct bearing on the costs and returns of the firm. An economic analysis of the problems facing the farmer involves consideration of each of these.

Farmers use chemical, cultural, biological, and other methods of insect control in the hope of realizing greater profits. Pests tend to reduce potential crop yields and quality, and, other things equal, reduce farm income.

Farmers may use insect controls because of an observable insect infestation and hope to reduce or eradicate the insect population and salvage their crops. However, the incentive for using insect controls and the actual decision to use them may not always be so direct. Controls are frequently used as an insurance against a possible or probable damaging infestation.

INPUT–OUTPUT RELATIONSHIPS

Although insecticides and other insect-control techniques contribute to greater production or improved quality, or both, the response from the controls differs from the typical direct output effect associated with other inputs, such as fertilizer, hybrid seed corn, and moisture. The typical response to insect control allows normal development of the plant or animal to occur by reducing or eliminating the pest, whereas with other inputs, such as fertilizer, the response is reflected in stimulated biological processes.

The effect of insects on yield and quality depends not only on the level of infestation but also on the level of the other inputs, such as fertilizer and moisture. Because of this interaction with other inputs, insect-control methods must be evaluated with respect to specified levels of the other inputs.

The development of insecticides and other insect-control methods has reduced the risk associated with the production of many crops. This has encouraged more intensive cropping systems, which use larger quantities of purchased inputs, such as fertilizer, than would have been used in the absence of insect-control systems. The over-all effect of these changes, combined with other aspects of modern technology, has resulted in increased agricultural production.

COSTS AND RETURNS

For more than a decade, farmers in the United States have been faced with rising costs for purchased inputs and falling or steady prices for their output. Those who have stayed in business attempted to maintain income by increasing production and hopefully increasing the total income received from the larger output, and by lowering production costs per unit of output. If the use of a given chemical or other control will either increase revenue with no increase in costs or maintain revenue at a lower cost, it is obvious that its use would be profitable to the firm. However, if costs and returns both move in the same direction, a more detailed analysis is required. Insect-control measures are an added cost of production. In addition to the costs of the insect-control materials, labor and equipment costs are generally increased.

In order to make a decision regarding the method of insect control to use, an evaluation of the quantity and quality of output obtained by the various insect-control measures is needed. This should be done for various levels of insect infestation. It is important to include an evaluation of the results of having no insect control. This is necessary in order to determine whether it pays to control insects at all.

Insect-control systems increase income by reducing insect populations, thus increasing yields or improving quality, or both. As the quality of the crop is altered, its value increases or decreases according to the way the market evaluates the change in quality of the product. The increase in production will often result in higher returns until the practices become widely adopted, and total production of the commodity increases significantly. The result will depend on the price elasticity of demand; there may be an increase in returns to the producer, no increase, or even a decrease.

Another potential benefit from the use of certain insect-control methods is that it may alter the date of harvest. This may enable the producer to sell his crop at a more favorable price. Costs of production could also possibly be reduced if maturity dates were altered to utilize labor more efficiently. The trend toward the development of pest-management systems promises to reduce input costs from their present level and at the same time maintain or increase output.

RISK AND UNCERTAINTY

Insect-control systems reduce the risk and uncertainty associated with the production of abundant supplies of high-quality food. They protect the producer from suffering large reductions in yield that may be caused by insects. Therefore, the producer does not have to contend with the possibility of incurring a large loss from insects in any given year. Insect-management systems tend to reduce this variation in yield and quality caused by insects, thus bringing about a reduction in the amount of uncertainty associated with production of a crop.

Currently, farmers have limited knowledge of the relative risks associated with different levels of pest control. They can only decide whether or not to use recommended control systems. In general, for many crops in selected areas it is more profitable to use complete insect-control systems than not to use any.

However, with information on the extent and frequency of damage related to particular pests, farmers may be provided with estimates of rewards associated with alternative pest-control practices. Economic rewards should be estimated for many degrees of pest control. They should range from no pest control to the use of a complete system of control. They should take into consideration the probability of an infestation and the cost associated with each level of controlling the infestation.

SOURCES OF DATA FOR ECONOMIC ANALYSIS

There are at least three basic sources of data that can be used for economic analysis: test plots, case studies of production units, and surveys. Each of these methods has advantages and disadvantages.

Test Plots

Data from test plots is probably the best available to obtain measurements of response to insect-control systems. Under controlled experiments it is possible to obtain precise measures of inputs, the interaction effects of inputs, and the response to insect control in terms of yield and quality.

Several problems may be encountered when test-plot data are used. Conditions in the plots may differ in the following ways from those that exist in many fields: (1) in plots only one kind of insect is usually studied, but in the field several different insect pests may be present; (2) test plots may receive a higher level of management than prevails under field conditions; and (3) plot data may not apply to actual production practices because of the interrelationship of pest-control practices on adjoining units in the field or because of pest-control measures used in the preceding production periods. These problems can often be overcome if they are taken into consideration when the experiment is designed. Test plots provide the only information source where many of the related factors can be scientifically measured and evaluated.

Case Studies

To obtain case-study data, records are kept over a period of time on a production unit to study the result of changes in the unit's production practices. This provides an opportunity to study the effects of such changes on the organization and income.

In these studies, one or more farms is selected as representative of certain units that use insect controls. The unit is then studied in detail. Records of physical inputs and outputs are collected to show the economic relationship of various control methods. If records are kept over a sufficient period of time, the economic situation before and after the adoption of insect-control measures can be established. From this information, conclusions are drawn concerning the profitability of the insect-control system used.

One advantage of the case study is that the unit of observation remains intact throughout the study and all forces can operate freely. Consequently, the observable results may be more meaningful. The case study is useful in appraising cause and effect relations within the unit. It could become an effective demonstration unit in extending the conclusions to other production units.

Disadvantages lie in the great amount of detailed information that must be kept and therefore the limited number of observations that can be handled. The influence of the manager and of other unmeasurable factors applicable to that particular unit may have a greater effect on the difference between the net returns of the alternative control practices than the controls themselves. Therefore, generalizations made from this type of study must be qualified.

Surveys

Information on production, production practices, inputs, attitudes, costs, and returns may be obtained by the use of surveys. Surveys are probably the quickest method of collecting a large amount of data. They can provide information on the nature of the insect-control practices being employed and the amount and type of equipment being used. They are of value in estimating the amount of insect control being applied, the number of acres being treated, and where the control is being used.

One of the principal disadvantages of surveys is the sampling error that can enter the data. To prevent such a bias, a sample of sufficient size to provide reliable data should be used. It is difficult to obtain response data from a survey, since suitable estimates of the level and composition of the insect infestation often are not available. It is also hard to obtain accurate estimates of variations in quantity and quality of the commodity produced under the particular insect infestation.

Data Needs

Data currently available from test plots for economic analysis are limited. Much of the research done in the area of insect control has been largely concerned with performance of chemical and biological controls in eliminating pests. In many cases, yield and quality data from the experiments have not been recorded. Estimates of losses caused by insects under various production conditions are vital for appropriate economic analysis. Not only the types of insects but the level of infestion should be reported.

Most plot trials consider only one insect, but under actual field conditions a plant is usually attacked by more than one. The cumulative damage from the insects is usually less than the sum of the damage of each insect, based on estimates of its destructiveness when no other insect is present. Thus, experiments need to be conducted considering combinations of pests that would approximate those conditions encountered in the field. Also, there is a large gap in the data demonstrating the effect insect controls have on the quality of the product. There may be a significant alteration in the percentage of the crop that is marketable in the various grades and thus sold at different prices.

Economic studies dealing with the value of insect controls to society will require more than information directly related to agricultural and forest productivity. Knowledge is needed on the total impact of control systems on the human environment.

ANALYTICAL TECHNIQUES

Analytical techniques for evaluating the use of control methods are suggested by the questions raised earlier. Specific questions on the economics of insect control will differ among the major decision makers. Some analytical techniques that may be used to provide answers for economic questions are: tabular analysis, game theory, production function analysis, budget analysis, and programming techniques.

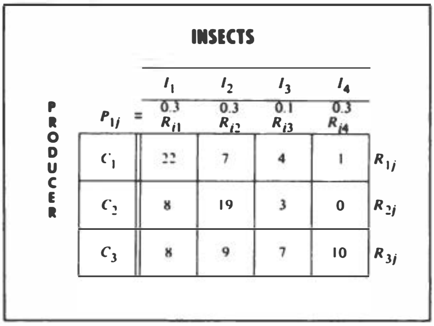
Tabular Analysis

With tabular analysis, information from case studies or survey data is summarized in tables. Observations are made about insect controls as they relate to production and to other inputs. These data may be used for a point in time merely to describe the use of specified insect controls, or, over a period of time the data may be used to describe changes. This type of information is often used to describe representative resource situations for either tabular or econometric analyses.

The advantage of using typical resource situations is that the effects of particular managers tend to "average out" and thus do not exert undue influence on the conclusions. This can also be said of other unmeasurable and random forces. Consequently, some inferences can be applied from the model to real production units. A disadvantage of using such resource situations is that results may not be applicable to any specific unit.

Game Theory

One approach to decision-making under conditions of risk and uncertainty is the use of game theory. The decision involves the selection of a method of insect control given various levels of insect infestation and their probability of



INSECTS

		I_1	I_2	I_3	I_4	
	P_{1j} =	0.3	0.3	0.1	0.3	
		R_{i1}	R_{i2}	R_{i3}	R_{i4}	
PRODUCER	C_1	22	7	4	1	R_{1j}
	C_2	8	19	3	0	R_{2j}
	C_3	8	9	7	10	R_{3j}

FIGURE 57
Payoff matrix.

occurrence. The profit, or payoff, is associated with selected methods of insect control for given levels of infestation and the probability of an infestation.

Given the levels of infestation (I_1, I_2, I_3, and I_4) that can occur, the alternative methods of insect control (C_1, C_2, C_3, and C_4), and the output response to the control measures—the price of the inputs and outputs—the profit or payoff matrix can be determined (Figure 57). P_{1j} represents the probabilities of the selected insect infestations I_i through I_j. The numbers included in the payoff matrix (R_{ij}) represent the profit per acre received by the producer when he employs the i^{th} control method and the insects are at the j^{th} level of infestation.

Let us assume that the producer is acquainted with the profit per acre associated with selected methods of insect control for different levels of insect infestation, that is, the information contained in the payoff matrix. For the present, also assume that the producer is a pessimist and attempts to maximize the minimum payoff. With this strategy, the producer will select control method C_3, because the other two methods have possibilities for lower returns.

Now assume that, over a period of time, probabilities of various levels of infestation were determined. These probabilities should be associated with the infestation in the preceding year and with weather conditions. By multiplying the profit per acre by the probability of that level of infestation occurring and summing horizontally across the payoff matrix, the expected value of the profit for each method of insect control can be determined. The general formula for computation is the following:

$$P_1 \times R_{0.1} + P_2 \times R_{0.2} + \dots\dots\dots + P_n \times R_{0.n} = \text{ expected profit per acre for one method of insect control.}$$

Using the numerical values given in Figure 57, the following example illustrates how the method of control yielding the largest expected profit per acre can be determined.

Method of Control		Expected Profit
C_1	0.3 x 22 + 0.3 x 7 + 0.1 x 4 + 0.3 x 1 =	9.4
C_2	0.3 x 8 + 0.3 x 19 + 0.1 x 3 + 0.3 x 0 =	8.4
C_3	0.3 x 8 + 0.3 x 9 + 0.1 x 7 + 0.3 x 10 =	8.8

In this case the producer would select C_1 as his method of insect control.

Production Function Analysis

Production function or input–output analysis examines observed or assumed relationships between variables. It is an expression of a technological relationship between the amount of product and the amount of factors of production needed to produce this product. The function states the average amount of product expected to be forthcoming given the levels of the inputs involved.

Holding the other inputs at some constant level, Figure 58 illustrates a hypothetical example of how alfalfa production might be related to insecticide use for a given level of insect infestation. With the application of insecticide in increasing amounts per acre, yields increase to a maximum of 5 tons/acre, but additional quantities of insecticide per acre do not increase the yields further.

Researchers can use this type of analysis to vary the intensity of insect controls and observe the changes in production. From the results, economists can establish rates at which the most profitable control is achieved. Using this approach, an individual producer with unrestricted capital should intensify control until the value of added production is equal to the added costs of control. This example assumes that all other inputs involved in alfalfa produc-

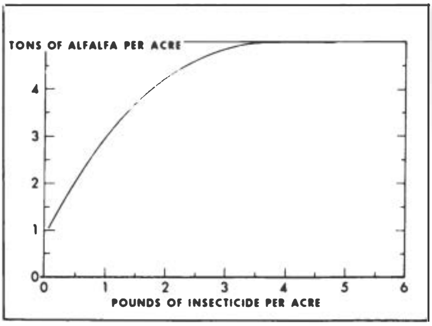


FIGURE 58
Relationship of alfalfa yields to insecticide use.

tion are held at some fixed level. The analysis also assumes that we have some given initial level of insect infestation.

However, as the initial level of insect infestation varies, a family of production functions is generated. The lower the initial infestation level, the smaller is the response to the insect control. If there is no insect infestation and other inputs are combined so that they produce a maximum yield, the production associated with different levels of insect control would be a horizontal line equal to the production without any control. Figure 59 illustrates what a family of production functions may look like given varying initial insect infestations. I_0 would represent no infestation; I_1 would represent some low degree of infestation. These infestations could be increased up to some high level, I_n. Therefore, it is evident that not only must the initial level of inputs be stated, but the level of initial insect infestation also should be specified.

Budgeting and Programming

Budgeting is a technique for quantifying the various alternatives available to the firm, so that a decision can be made as to which alternative is most profitable to the firm. It can be used in varying degrees of complexity, from a partial budget dealing with problems such as replacement of a piece of equipment to a complete budget of the entire farm operation. Partial budgeting is concerned with estimating the net returns from some segment of the production unit. Complete budgeting refers to formulating a plan for all the decisions associated with the production unit. In other words, in a complete budget the net return for an entire production unit is analyzed. Through comparison of several complete budgets, the optimum organization of the production unit can be determined.

The question of whether or not a producer should use an insect-control method for a specific crop could be analyzed by the use of partial budgeting. The analysis would need to consider the change in net returns resulting from adopting the control measures. This change in the farm business can affect

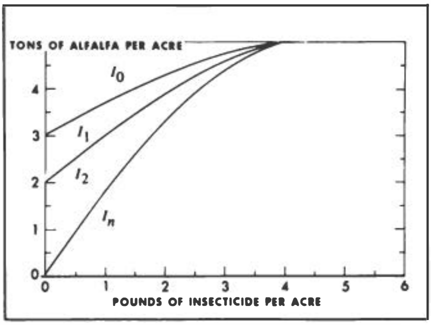


FIGURE 59
Relationship of alfalfa yields to insecticide use with various levels of insect infestation.

income in one or more of the following ways: income—increasing: (1) additional returns, (2) reduced costs; or income—reducing: (1) additional costs, (2) reduced returns.

If the income-increasing effect is greater than the income-reducing effect, it is profitable for the producer to adopt the insect-control measures. Partial budgeting considers factors affecting each of the above items, but only those factors which actually change. Similarly, in deciding between two or more methods of insect control, partial budgeting can be used to compare the effects on net returns of employing the alternative systems. Such uses of partial budgeting depend on relevant prices of inputs purchased and products sold.

Linear programming is an efficient systematic procedure for examining a large number of enterprises for a production unit and selecting the combination of activities that satisfies some criterion, such as maximizing profit or minimizing cost. While linear programming techniques are of recent origin, they have been used extensively. The basic principles involved are those of budgeting. The usefulness of the technique arises from its capacity to process a large number of alternatives in a single problem. It is possible that linear programming techniques could be used to analyze the most efficient combination of insect-control methods for a given production unit.

AGGREGATIVE ECONOMIC IMPACTS OF INSECT-CONTROL SYSTEMS

The Environmental Pollution Panel of the President's Science Advisory Committee has estimated the value of some of the insect-control programs that have been employed in the United States. The following paragraphs are quoted from pages 273–275 of its report (see the Bibliography at the end of this chapter).

> "Approximately 50 million acres of wheat are seeded each year in the United States and 30 million of this is in areas infested by the Hessian fly. Of this amount approximately 20 million acres are within the area where serious losses would occur each year if some method of Hessian fly control was not practiced. An estimated 4,000,000 acres are grown in the Hessian fly infested areas where wheat would furnish valuable fall and winter pasture if it were not damaged by this insect.
>
> "Even with the use of present Hessian fly control methods, there is an estimated loss in grain of 1.7% or $32,000,000 in the U.S. each year. This does not include the estimated $6 per acre loss in fall and winter grazing in the southern portion of the Hessian fly infested area.
>
> "*Control methods for Hessian fly.*—There are three principal control measures available for the Hessian fly: (1) delay seeding until the fall brood has disappeared, (2) chemical control, (3) planting Hessian fly resistant varieties.
>
> "*Value and cost of various control measures.*—Loss if no control measures were practiced: It is estimated that the average yield reduction on the 20,000,000 Hessian fly in-

fested areas [sic] would be 18% by the fall brood (*Jour. Econ. Ent.* 53:501–503) and 4% by the spring brood or a total of 22% if no control measures were practiced. This loss would amount to 83,600,000 bushels per year (average yield of 19 bushels per acre) or $167,200,000 (average value $2.00 per bushel). In addition, there would be an estimated $24,000,000 loss per year in grazing value (4,000,000 acres at $6.00 per acre). Therefore the estimated loss each year due to Hessian fly would be $191,200,000 if no control measures were practiced.

"Control by delayed seeding: Delayed seeding is an effective method for control of the fall brood of Hessian fly but does not prevent damage by the spring brood. From available information it is estimated that if delayed seeding was not necessary to control the Hessian fly an increase in yield of 3% could be expected from wheat planted at an earlier date. Therefore if we had to rely entirely on delayed seeding for Hessian fly control, and if this practice was applied on all the 20,000,000 acres the loss due to Hessian fly would still be $53,200,000 in grain (20,000,000 acres x 7% loss x 19 bu. yield x $2 per bu.), and $24,000,000 in grazing (4,000,000 acres x $6) or a total of $77,200,000. Since the loss if no control measures were available is estimated at $191,200,000, the value of delayed seeding for Hessian fly control has a potential value of $114,000,000 a year ($191,200,000–$77,200,000).

"Cost of developing and maintaining delayed seeding method of control: The delayed seeding method of control has been in use for many years and is based on a knowledge of the biology of the insect. We estimate that 10 man-years per year (5 entomologists and 5 agronomists) for 20 years were involved in developing this control method. The cost per man-year (from 1915 to 1935) is estimated at $10,000 per year. Therefore, the total cost of developing the delayed seeding method would amount to $2,000,000. Although the fly-free date is well established for most areas, a few states maintain a service to inform the farmers of the fly-free date each year. It is estimated that this service amounts to $20,000 per year. We therefore have a potential saving of $114,200,000 per year for a *total research cost* of $2,000,000 and a maintenance cost of $20,000 per year, about $55 per year for each dollar invested in research.

"Control by chemicals: Although some of the systemic chemicals give excellent control of the fall brood of the Hessian fly, chemicals have never been used on a commercial scale for control of this insect. This is because other methods are as effective and are much cheaper. Chemicals for the control of Hessian fly would cost about $3 per acre for the material and $1 per acre for application. If the entire 20,000,000 acres were treated the cost would be $80,000,000. Since this method only controls the fall brood, there would be a 4% loss by the spring brood or $30,400,000. Treated wheat could not be grazed so there would be a loss of $24,000,000 in grazing value, or a total cost and loss of $134,400,000. Since the loss if no control measures were used is estimated at $191,200,000 chemical control measures could still save the growers $56,800,000 per year, less than $2 for each dollar invested. In the absence of other control measures, growers in the more critical areas would no doubt use chemicals but many would accept the losses without treatment of any kind.

"Cost of developing chemical control measures: Only a few individuals have been engaged in developing chemical control measures for the Hessian fly, so the total cost in developing this method has probably not been more than $200,000.

"Control by resistant varieties: The growing of resistant varieties is the ideal method for controlling the Hessian fly. If satisfactory agronomic varieties possessing resistance are available, this method can be used at no extra cost to the grower, without creating a residue or other toxicological hazards and without upsetting nature's balance between insects and other natural enemies. Seed can be planted at the optimum time, and there is no loss in fall and winter grazing. Varieties can be developed which are practically im-

mune to Hessian fly attack so it would be possible to prevent the entire potential loss of $191,200,000.

"Cost of developing and maintaining resistant varieties: The first concerted effort to develop Hessian fly resistant wheats started in the 1920's. Since that time an estimated 300 man-years (Federal and State entomologists, breeders, pathologists) have been devoted to this research effort or a total of $6,000,000 (300 x 20,000 per year). An estimated $210,000 a year is now devoted to developing Hessian fly resistant varieties."

Economic theory suggests that some questions can be raised regarding the validity of the estimated benefits and losses obtained in this type of analysis. Aggregative economic considerations of the impact of insect-control systems are related to the over-all changes in production and prices for the product brought about by the adoption of the control system. When the use of a control system increases yield or quality, or both, the individual producers typically think of this in terms of increased income. However, it shall be seen that this may not be the case.

We will assume that the adoption of a new insect-control system increases output of the product. The few early adopters of this new practice will reap the benefits of the innovation in terms of increased total income, because the increase in total output from these producers is small and will have no effect on the price of the product. As the practice becomes more widespread, total production will continue to increase, and prices received for the product will be depressed. The net result of this increase in production will depend on the elasticity of demand for the product. If the demand for the product is inelastic, total revenue to the producers will decline; if the demand for the product is elastic, total revenue to the producers will increase. As a result of the adoption of this new insect-control system, which increased total output, the consumer benefits by having more of the product at a lower price.

IMPACT OF GOVERNMENT ACTIVITIES ON USE OF INSECT-CONTROL SYSTEMS

Because of its responsibility to society, government at various levels is concerned with insect control and its impact on society. Some areas of governmental concern are preservation of human health, protection of wildlife, productivity of agriculture and forestry, and organization and location of production.

A benefit–cost analysis would be useful for providing economic guidelines for governmental agencies that make policy decisions related to the kinds of research undertaken and to regulating insect-control methods. Because this research and these regulations affect a larger segment of our society than just those using the insect-control system, a comprehensive study of the associated costs and benefits to society as a whole should be undertaken.

Policy decisions related to public funds used for research should be directed to those areas that yield the largest returns to society for the money spent consistent with long-term objectives. Recently, in an effort to fulfill these objectives, additional funds for research have been directed to studies emphasizing biological control. Policy decisions may also take the form of restricting or eliminating the use of selected control methods when there is either an alternative insect-control system available or no alternative insect-control system available.

If an insect-control system is removed from the market when there is an alternative method of control available, there will probably be an alteration in the costs and returns of producing the product. Policy decisions may also take the form of restricting specified methods where effective alternative systems are not available. In such instances, the reduction in net income to individual producers reflects the difference in profitability of the next best alternative. The changes in profitability may result from changes in costs and returns associated with substituting one crop for another, from producing the crop without the control system and substituting another control system, or from changes in crop rotations and the associated livestock enterprises.

Economic considerations related to banning the use of specific insect controls are unique in that analyses have not been made for other unit inputs. The economic problems associated with banning a particular control method have different effects on individual producers than on society as a whole. Specific insect controls are banned with the assumption of achieving a net benefit to society. Society benefits from a reduced hazard when government bans insect controls that are considered harmful. However, removing an effective, low-cost control method from the market usually means higher production costs to the farmer, which results in higher food costs to the consumer. Thus, society may also suffer when certain insect controls are removed from the market. Governmental supervisory agencies need to consider and evaluate these factors in deciding whether to remove or approve the control system.

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CHAPTER 19

Organization and Education

ORGANIZATION

The organization of personnel for insect-pest management and control may be divided into two groups: individuals primarily interested in education or research, or both, in pest management and control; and individuals who are primarily operational and perform the operations of pest management and control.

RESEARCH AND EDUCATION

The organization of universities, the primary setting for professional training in insect-pest management and control, should create the best possible environment for instruction, learning, and research in the many phases of this area of knowledge and activities. In the university organization, sufficient instructional personnel should be made available to provide students with the multidisciplinary background that is so essential to a good pest-management and control educational program. A minimum of four professionals in each discipline might be considered necessary for the most effective exchange of viewpoints and ideas.

To provide maximum learning and research opportunities at the least expense, the administration of the university should provide coordination of activities and good communications. The program should be organized so that enthusiastic and authoritative instruction and creative and productive research are initiated, stimulated, and rewarded. Research results should be promptly disseminated, and the administration and faculty should be alert and responsive to new needs in teaching and research. The university needs to encourage the faculty and research workers to keep abreast of the changes taking place in scientific knowledge. Continuity of personnel and programs should be fostered.

The university needs to be organized so that adequate instructional and research assistance, facilities, equipment, and instrumentation are available. Maintaining a balance between basic and applied instruction and research is required. Interdisciplinary and team approaches to both instruction and research should be encouraged. Land-grant universities should be organized to coordinate programs effectively and to facilitate communications between the resident instruction, extension, and research staff members. It is essential that the university provide good library-reference, chemical-analytical, statistical, insect-identification, and computer services. Cooperation with commercial companies dealing with insect-pest management and control is most desirable.

Governmental research agencies, other than universities, private foundations, and commercial companies are continuing to conduct valuable scientific research and to render good service in the application of research contributions to insect-pest management and control. They should be organized to provide the same research climate, services, and facilities as the universities.

PEST MANAGEMENT AND CONTROL OPERATIONS

The organization of insect-pest control operations varies greatly in size and nature. An individual may perform an occasional pest-control operation on a part-time basis. Conversely, many trained workers may be employed in one organization, and they may use airplanes and specialized equipment in a local, national, or international program to control insect pests over wide areas.

Regulatory controls, including quarantines and pesticide regulations, are organized by government agencies. In quarantine operations, adequately trained personnel are stationed at points of possible entry to intercept incoming pests. In carrying out insect-pest suppression or eradication campaigns, national and local government employees cooperate with private individuals and commercial companies. The identification of insects collected in these programs is done mainly by staffs at government laboratories or at museums and universities. The staffs consist of specialists in different groups of insects. There are also private individuals who identify insects and other arthropods in specific groups. In the agencies concerned with pesticide regulations, data on insecticides to be offered for sale are carefully examined. The accuracy of the label and the purity and effectiveness of the contents of the packaged product are determined by a staff trained in this work.

Insect surveys are usually organized as government or university programs, but they frequently involve voluntary collaborators interested in insect populations or outbreaks. Forecasts of insect-pest outbreaks and the need for control are generally based on surveys that keep in close touch with specific insect-pest populations and the factors affecting them. Commercial companies also perform survey services.

Discovering and developing host resistance to insects are usually cooperative activities carried out by a team composed of a geneticist, an entomologist, and a plant or animal breeder. Sometimes the team includes a biochemist, who may be assisted by a plant explorer. Universities and government agencies support such teams, as do commercial companies in some instances. Seed of the insect-resistant varieties that are developed is customarily sold through commercial channels.

The utilization of biological control parasites, predators, pathogens, and competitors in insect-pest management and control operations is more often carried out by government (national or local) agencies, although some commercial companies operate in this field. Some of the biological control programs are handled by organizations that are international in scope.

Cultural control of insect pests is usually performed by an individual operator, who includes the practice in his cultural operations. It is usually more effective when organized on a community-wide basis. In some cases, especially those in which insects affect man's comfort and health, cultural control is included in pest-suppression programs.

Chemical and mechanical methods and combinations of various types of insect-pest management and control are organized in a variety of ways and vary in complexity. Insecticides, which are a major item in insect control, are usually developed and manufactured by companies that manufacture other kinds of chemicals. They are distributed through formulators, wholesalers, and retailers. Various insect attractants and repellents also are produced by the chemical companies. Machinery for applying insecticides is generally manufactured by companies that make other machinery, and is sold through normal trade channels. Insecticides are applied by self-employed persons, or by commercial companies, or by government agencies.

Commercial pest-control companies serve the public by the control of termites, cockroaches, carpet beetles, and other insects that infest dwellings and industrial buildings.

Mosquito-abatement districts are organized in many places. These are usually government operations, often local government, designed to reduce the mosquito problem in a given area. Cities also have pest-control units that operate to reduce fly populations and other insect nuisances and to protect shade trees and other ornamental plants from insect damage.

To summarize, insect-pest management and control organizations are as many and varied as are needed to meet the problems.

EDUCATION

Formal training in insect-pest management and control serves as a basis for future growth and development. It is an important factor in developing competence in this dynamic and changing field. To be successful, an entomologist must continue his quest for knowledge and skill throughout his career. He should be skilled in writing and speaking. He should have a working knowledge of mathematics, chemistry, and other physical sciences. Training in social sciences and the humanities, which enables an individual to fit into and function well in his community, should be included in every study plan.

Although insect-pest management and control is accomplished in the field, much of the basic work leading to practical application is done in the laboratory. As a result, there is a trend toward more laboratory and less field work in training programs. However, field experience is essential to the trainee, and curricula should be designed to give students a balanced participation in laboratory and field work. Temporary employment experience with a university or with a government or commercial agency is highly desirable to supplement formal academic work. A season at a field laboratory or branch station is often a useful part of a graduate student's experience.

The student and the teacher are the most important ingredients of a training program in insect-pest management and control. Success of the program depends on intelligent, persevering students and competent teachers full of enthusiasm for the subject and with genuine interest in the welfare of the students.

TRAINING IN PEST MANAGEMENT AND CONTROL

Pest management is a relatively new concept. It has many well-established roots in the past, and its evolution and emergence from the traditional considerations of insect-pest control, especially in relation to the various control approaches, was inevitable. It now occupies a position on the leading edge of imaginative thought in entomology. The concept did not evolve because of philosophical advances by students or by teachers in entomology; rather it evolved from new approaches made by research workers, especially those charged with responsibility for controlling insects and related pests. It is understandable, therefore, that it is not yet fully supported in depth by training programs in entomology; training programs have not had time to adjust to new needs. Modern training programs are necessary to provide the kinds of researchers required for pest-management research and operations in the future.

The multitude of themes on pest-management systems discussed in this book are brought together in Chapter 17. These themes are woven into a philosophical fabric that displays the concept of pest management. By inference, they also make plain the kinds of training and experience that will be essential to further progress of this concept.

Basic Biology

A broad background in general biology is basic to specialized training in entomology. Entomologists are biologists who choose to concentrate their professional activities within the almost boundless limits of the insect world. Many institutions recognize this need by requiring broad and comprehensive training in biology prior to extensive training in entomology. If a student anticipates graduate study, undergraduate specialization beyond enough training to introduce him to the various aspects of entomology may be undesirable.

General Entomology

Whatever innovations are required to educate future specialists in pest management must rest firmly on a foundation of training in general entomology along traditional lines—insect morphology, systematics, ecology, biology, physiology, and behavior. Without this firm background, those intending to go on in pest management will find themselves without the required building blocks. It also is necessary that background training be obtained in the rationale and methodology of the various major approaches to insect-pest control. These approaches are the components that make up the management system, and the student must be familiar with their bases and with their strengths and weaknesses.

Training for Research

We can now consider the specific demands that research in pest management makes on training programs in entomology.

Major requirements of an educational program for research scientists in insect-pest management are training in: (1) applied entomology and pest management; (2) population ecology; (3) the systems approach to management problems; and (4) integrating host resistance and other controls into pest management.

Pest-Management Philosophy

Modern training programs in entomology must not be content to stop at adequate education in the techniques of control approaches. In addition, they must go on to reveal such techniques as components in an eventual management system and to relate them with one another. This can probably be accomplished best at the level of graduate or postgraduate seminars where the emphasis is not on the transfer of information from teacher to student but rather on catalyzing the development of a point of view in the individual student. The rationale should be challenged and explored by the student, to determine for himself if it is realistic and workable. The student should also determine whether it fits into his future professional career as he thinks it will develop and whether there are reasonable and satisfactory alternatives to pest management in meeting the agricultural and forestry needs for insect control in relation to the total environmental background. The kinds of biological and ecological information required for the design of integrated management systems should be explored and discussed, and ways in which this information can be gathered through observation and experimentation should be considered. Frequently, theory in a science outstrips our ability to support it with facts, because adequate methods of data collection are lacking. This may come to be the situation with theories in pest management, and considerable attention should be given to sampling and data-collection approaches and to their adaptation to pest-management problems, to the automation of data collection and recording, to shortcut methods such as sequential sampling, to techniques such as life tables, and to techniques that will permit simple monitoring of established pest-management systems. In short, new elements must be continually introduced into training programs that will orient the students' thinking and accumulated knowledge to the principles of insect-pest management.

Population Ecology

Population ecology is an area of specialization in entomology just beginning to gain significant recognition and support, and one for which a new generation of teachers and researchers is now beginning to emerge. Its emphasis on the fluidity and dynamic nature of populations and its concern with the regulatory mechanisms that operate on and within populations, the interactions between populations, and the relations of populations with their environments are central to the pest-management philosophy. Without appreciation of this viewpoint, the design of management systems can hardly be accomplished, and, without research competence in the entire general field of population science, the information and data essential to the system cannot be obtained.

One of the major prerequisites to meaningful courses in insect-population ecology is a knowledge of certain fields in mathematics, chiefly calculus, and the ability to relate this to biological programs—biomathematics. Students in entomology who wish to conduct meaningful research on population ecology need not be experts in mathematical research as well. However, they do need to have a basic understanding of certain fields of mathematics and to know when to seek expert assistance and advice in designing research or interpreting results.

Another major need in training in insect-population ecology is the integration of information from a wide variety of allied and related fields of specialization. One must either have a good grounding in subjects such as general biology and ecology, physiology and nutrition, genetics, bioclimatology, energetics, and evolution or become thoroughly familiar with the salient features of these as they bear on population ecology.

Systems Design and Analysis

To be successful in pest-management research, the student must have some insight into and understanding of pest-management systems, which are discussed in Chapter 17. One recently proposed solution is to incorporate what must be known of systems into a course on mathematical ecology. Without going into detail here, it will suffice to say that this course should progress from a consideration of ecosystems with their two principal components, the environment and the biota, to a study of resource and habitat and machinery variables.

Discussion

To incorporate all these needs into an over-all training program with reference to research on pest management will not be easy. However, the stimulation for curricular modifications should come from a recognition of the tremendous challenge presented by the economic necessity of developing pest-management systems and the high-quality research on which they will have to rest. We do not state categorically that all entomologists active in pest-management programs must have the in-depth training indicated in this chapter. Some, the operators and managers of such programs, probably need only nodding acquaintance with population and systems ecology.

TRAINING FOR EXTENSION

Extension personnel must have the ability to interpret research results and other knowledge and present them to the public in practical form. Consequently, extension work in entomology involves not only the science and technology of the profession, but also public relations, economics, sociology, the use of all available communication media, and other factors, in dealing with both rural and urban people. Thus, the need is evident for training in such areas as extension methods, communication, and economics, as well as applied entomology. Course work that would introduce the student to these various subject-matter areas and pursue his special interests more fully should be useful.

TRAINING FOR SPECIALIZED CONTROL

Some insect-pest control is practiced by almost everyone, from the housewife to the professional entomologist. However, this discussion is mainly on training programs for those engaged directly in control work on a professional basis. Some of the principal groups involved include pest-control operators, custom spray applicators, industrial personnel employed in public relations–sales–control work, government agencies engaged in large-scale control or eradication programs, and local and national regulatory programs involving inspection, survey, and quarantine. The type and level of specialized training vary considerably in the several areas.

When emphasizing training needs at the university level for future workers in pest management, we should not overlook equally pressing needs for the education of pest-control specialists and others at the operational and supervisory field levels for training in the principles of pest management. Much of the economic and entomological success of future management programs will rest on the acceptance by supervisory personnel of such principles as spraying only when necessary and relating damage to economic thresholds. Consequently, training of control specialists in the new philosophy is vital to success. This means that the broad picture of management systems must be painted clearly and vividly even in paraprofessional curricula and in those designed primarily for applied workers and students that terminate at the bachelor's or master's levels.

Employees in industrial control work involving sales and public relations may not require highly specialized training within the field of economic entomology. They are usually involved in a broad area concerned with all phases of pest control, including weeds, plant diseases, and plant-infesting nematodes, as well as insects. The employer provides intensive training in the technology directly required in the position. University training should emphasize basic sciences, communication, economics, bionomics, and related subjects. As the field becomes more complex, it appears probable that higher levels of training will be required.

Training for employment in large-scale insect-control programs is generally parallel to that in extension. Whether the project involves a local or national government agency, the work not only requires a high level of proficiency in pest control but also involves public relations, use of communication media, and economics.

Training for regulatory work should provide courses in basic sciences, entomology, communication, statistics, and cultural subjects. Knowledge is also required in the areas of insect systematics, ecology, physiology, and toxicology. Foreign assignments may require special language skills.

Intensive in-service training in the technology of the job is often given to individuals whose activities will be limited to specific jobs. Earlier training in biology and entomology may be needed in these positions when they require technical knowledge. In other more routine jobs, however, training in biology or entomology would be mainly of value as background.

NEED FOR INSECT-PEST MANAGEMENT AND CONTROL IN THE FUTURE

The progress that has been made in entomology in recent years will undoubtedly continue at an accelerated rate. The greatest single influence will be changing agriculture and living standards. The rapid increase in population will necessitate doubled and redoubled efforts to keep pace with food and fiber requirements. Continued efforts will also be necessary to reduce costs of insect damage to maintain a place in a competitive market. Problems of insect resistance to insecticides, insecticide residues, and rising costs all dictate the need for more sophisticated approaches to pest control. Broader training and background will be necessary for the entomologists of the future if they are to apply research findings of other disciplines to insect problems and teach these techniques to succeeding generations of scientists. Interdisciplinary, problem-oriented, integrated control approaches will be utilized increasingly. As knowledge expands, the talents of research and extension teams will be brought to bear on specific insect problems in commodity production, marketing, and utilization.

National programs committed to the principles of consumer service, rural community improvement, and natural-resources protection will require added work in insect-pest management and control in the fields of recreation, conservation, and public health. Entomologists will be called on to help in the training of scientists of developing countries as well as in the solution of international and domestic insect problems. The functions of teaching, research, and extension in the universities will become less distinct. Extension and industry personnel are assuming a more important role in developmental research and product evaluation and in identifying new needs and problems. There is an increasing demand for entomologists in industry and regulatory work, occasioned by a burgeoning world commerce. All these factors clearly demonstrate the need for greater numbers of better trained and more highly motivated entomologists.

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