THE EFFECT OF LOW TEMPERATURE ON GROWTH AND BOLTING OF CABBAGE (*BRASSICA OLERACEA* VAR. *CAPITATA* L.)

by

Sandile Manzi Ngwenya

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Supervisor: Prof P. Soundy
Co-supervisor: Prof P.J. Robbertse

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DECLARATION

This dissertation has been composed by myself and has not been accepted in any previous application for a degree. It is a record of the work that has been done by me and all sources of information have been acknowledged by means of references.

Signed: …………………….   Date: ……………………

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BY

S.M. NGWENYA

SUPERVISOR: PROF. P. SOUNDY
CO-SUPERVISOR: PROF. P. J. ROBBERTSE

DEPARTMENT: PLANT PRODUCTION AND SOIL SCIENCE

DEGREE: M.Sc. (AGRIC) HORTICULTURE

Abstract

Cabbage is one of the most important cash crops which can contribute to food security. It is a cool season crop and its production maybe seriously impaired by bolting. Therefore, understanding cabbage bolting as affected by low temperature is vital for the sustainable production of this crop in South Africa. The objective of the study was to determine whether bolting in cabbage plants is triggered by low temperature during the seedling, cupping, early heading or mature head growth stages.

The research was conducted at the University of Pretoria's Experimental Farm and the Plant Science Complex. Walk-in growth chambers, glass houses, shade nets, incubators and the open field were used for conducting experiments in 2012 and 2013. Cabbage plants at different growth stages were exposed to different combinations of low (night) and high (day) temperatures. Night temperatures of 5 °C, 7 °C, 10 °C and 15 °C were used whilst 15 °C and 20 °C were used as day temperatures during the treatment phase. Night temperatures of 20 °C and day temperature of 30 °C were used for growing the plants after treatment. For Experiments 1 and 2, plants were transplanted into open field after treatment. A second field experiment was conducted separately to over-winter the plants. Plants were exposed to the same agronomic practices in the field. Harvesting for all experiments was carried out after plants reached full maturity. Parameters used for this research were head mass and length, core length, core width, and signs of bolting.

The results of this study showed no signs of bolting on hybrid cabbage plants during the seedling and cupping growth stage, however, signs of bolting, such as inflorescence primordia and developing inflorescences, were found in leaf axils along elongating cores and apical buds, on early heading and mature heads. This showed that both, the early heading and mature head stages were receptive for induction to bolting. From this study, it can be recommended that in areas that may experience instant transition from cold winter temperatures to warm spring temperatures, over-wintering of susceptible cabbage cultivars should be avoided to minimise the effect of bolting in cabbage production.

Key words: Growth stages, inflorescence, over-wintering, bolting, induction

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LIST OF KEYWORDS AND DEFINITIONS

Average maximum temperature	calculated from maximum temperature readings
Average minimum temperature	calculated from minimum temperature readings
Bolting	untimely development of the flowering stalk
Core	plant stem before reproduction phase/ seed-stalk after reproduction phase
Early head growth stage	growth stage during which plants initiate head formation (head still not firm when pressed with fingers)
Head length	length between head base and head apex
Mature head growth stage	period when cabbage head is firm when pressed with fingers and leaves fully packed within the head
Over-wintering	exposure of plants to low winter temperature regimes and harvested during spring season
Seedling stage	growth stage from emergence to transplanting
Temperature regimes	Temperatures to which plants are exposed to
Cupping stage	growth stage from transplanting to head initiation/folding of leaves

GENERAL INTRODUCTION

Cabbage (*Brassica oleracea* var. *capitata* L.) is one of the most important leafy vegetables grown worldwide (Adeniji *et al.*, 2010) and (Zur *et al.*, 2003). It belongs to the family Cruciferae. It was first discovered as a wild cabbage, a leafy winter annual native to Europe, growing along the coast of the North Sea, English Channel, and Mediterranean Sea (Pierce, 1987), where it has been grown for more than 3000 years and is adapted to cool moist conditions (Adeniji *et al.*, 2010). The ancestral cabbage was an annual, while the heading form is strongly biennial. A soft-headed cabbage was reported in ancient Rome and then introduced to the British Isles. The hard-headed cabbages were not mentioned until the ninth century. Thereafter, wherever it was introduced, cabbage was quickly adopted and cultivated (Pierce, 1987).

Early use of cabbage was medicinal, a treatment for gout, stomach problems, deafness, headache, and hangovers (Pierce, 1987). Cabbage is a popular vegetable that is used for cooking and is also known for its medicinal properties and supposedly contains chemicals that can prevent cancer. The history of its uses can be traced back to the Greek era, where the Greeks used fresh white cabbage juice to relieve sore or infected eyes. During those times, the Romans and Egyptians would drink cabbage juice before meals to prevent intoxication. Cabbage has the following benefits: 1. Anti-inflammatory vegetable; 2. Contains lactic acid that acts to disinfect colon; 3. Can also be used to reduce headache; 4. Another benefit of cabbage is its anti-cancer properties and is also said to be used for treating other skin conditions and 5. Drinking cabbage juice extracts is a good remedy for ulcers. According to Okoye (2010) some of the precautions to be taken into consideration when using cabbage is not to eat red cabbage raw, to avoid cabbage if you suffer from goitre, or take Monoamine-oxidase inhibitor (MAOI) antidepressants and cooked red cabbage can cause constipation and irritation of the colon (DAFF, 2010).

Cabbage is not particularly high in vitamins and minerals, but, because of the volume consumed, it contributes substantially to the average daily requirements (Pierce 1987). Cabbage is cultivated for its head, which consists of water (92.8%), protein (1.4 mg/100ml), calcium (55.0 mg/100ml) and iron (0.8 mg/100ml) and is eaten raw in salads or cooked (Adeniji *et al.*, 2010). Cabbage in South Africa is used for making i) salads, ii) soup, iii) ink, iv) cabbage atchar, v) canned as prickled cabbage and vi) some is frozen for later use (DAFF, 2010).

Cabbage breeding and seed production takes place outside Africa and no landraces exist. Seed is imported from Europe and Asia and is sold by seed companies and other retail outlets. Important horticultural characters for cabbage are head size, shape and firmness, taste, resistance to bolting, late flowering and maturity. Evaluating cabbage varieties for adaptation and yield will help farmers, breeders and seed companies to select and develop varieties best suited to the local environment and market (Adeniji *et al.*, 2010).

The importance of heading cabbage in tropical and subtropical regions has increased considerably in recent decades. Recent estimates indicate that in Africa, up to 100,000 ha are annually planted with heading cabbage (van der Vossen & Seif, 2004). Based on sales of commercial seed, at least 40,000 ha of white-headed cabbage is grown in Kenya, Uganda and Tanzania; 10,000 ha in Malawi, Zambia and Zimbabwe; 40,000 ha in Ethiopia; and 30,000 ha in Cameroon. Almost all white-headed cabbage is produced for local urban markets. Mozambique imports considerable quantities of heading cabbage from South Africa and until recently also did so from Zimbabwe (Adeniji *et al*., 2010). Globally, China is a leader in production of cabbages, followed by India and the Russian Federation (DAFF, 2010).

Cabbages are produced in all provinces of South Africa but the production is concentrated in the Western Cape, KwaZulu-Natal, Eastern Cape, Gauteng, Free State and North West Province (DAFF, 2010). Most cabbages are produced for domestic consumption. Fresh cabbages are sold through fresh produce markets, processors, restaurants, hawkers, retailers and chain stores. South Africa is self-sufficient in terms of cabbage production and the surplus is also exported (DAFF, 2010), but is not a major cabbage exporter. It represents 0.13% of world exports and is ranked number 36 in the world. South African cabbage exports in 2008 were destined to the United Kingdom: 52%, Netherlands: 15%, and bunkers: 10%, Angola: 5%, Mozambique: 5%, France: 3%, Mauritius: 3%, DRC: 2%, Japan: 2%, Switzerland: 1% and other: 2% (Source: Trade Map, 2008).

Cabbage grows well on a range of soils with adequate moisture and fertility. It tolerates a soil pH range of 5.5 to 6.8. To maintain growth, cabbage requires a consistent supply of moisture, and should as a general rule receive a minimum of 2.5 cm of water per week. It is highly tolerant to freezing temperatures, depending on growth stage, but less so to excessive heat. The optimum temperature for growth is 15 to 18 °C. In areas of mild winters, it will flower and complete its life cycle in the second year. Cabbage heads are ready for harvest 80 to 120 days after germination, depending on genotype and climate. With proper management, cabbage can produce 25 to 30 t/ha (Pierce, 1987).

Martinez-Zapater & Somerville (1990) mentioned that light quality, photoperiod and low temperature are the most important environmental factors which affect the onset of flowering in plants. Significant efforts have been dedicated to characterize the ways in which different plants are induced to flowering and respond to these environmental factors.

Hara & Sonoda (1982) stated that improved cabbage varieties have brought an increase in temperature tolerance, and thereby cabbage production became feasible in many areas. Head formation is affected by seasonal environmental conditions and temperature is the most influential factor. Cabbage as a biennial plant requires exposure to low vernalizing temperatures for flower induction (Pelofske & Baggett, 1978). Thomas (1980) emphasized that plants cannot become reproductive immediately after germination, but need to go through the juvenile phase before the plants can flower in response to cold.

Mero & Honma (1984) and Wiebe *et al.* (1992) independently mentioned that temperature is the main environmental factor affecting cabbage bolting and there is a great variability on vernalization requirements on different *Brassica* species. Induction to bolting and flowering depends on the degree and the duration of low temperature. Nanda *et al*. (1996) stated that exposure of plants to cool temperature can promote rapid growth and development thus leading to bolting. Yui & Yoshikawa (1991) also stated that when plants are exposed to chilling conditions for longer periods of time, plants will tend to flower earlier than normal.

High temperature after vernalization may delay or stop flowering induction (devernalization). Continuous exposure of cabbage plants with strong devernalizing capabilities (less susceptible to bolting) to optimum vernalizing temperature is not sufficient to induce bolting, if the plants are subsequently exposed to warm temperatures. Temperature affects the physiology of seedlings and subsequent plant growth (Muleke *et al.*, 2013). Hiller *et al.* (1979) also stated that interactions of endogenous phyto-hormones in plants form part of the many factors that affect bolting.

A considerable amount of research has been conducted on the effect of temperature on cabbage growth and bolting, mainly on Chinese cabbage. Valuable information has been received from these research conducted on Chinese cabbage. Such information gives insights on conducting further research on other crops. Green cabbage (regular, round and firm head) has been used on the present research.

Hypothesis

1. Cabbage bolting is triggered by low temperature during the seedling and cupping growth phases.
2. Cabbage bolting can also be triggered during the early heading and fully headed growth stages.

Objectives

1. To determine cabbage growth stages that are susceptible to be induced to bolt after exposure to low temperature regimes.

2. To determine the time taken by cabbage plants to initiate the formation of reproductive structures after being exposed to vernalizing temperatures.

Important notes

I) In most of the literature cited, the expression 'seed stalk formation' is used to refer to the process of flowering or bolting. According to strict botanical concepts, the mentioned expression should be regarded as a misnomer since a seed stalk should refer only to the inflorescence axis (scape) after flowering, fruit set and fruit maturity. The term 'bolting' will therefore be used throughout the dissertation to refer to the process of untimely inflorescence development instead of 'seed stalk formation'.

II) Figure i presents cabbage production areas in South Africa which were affected by bolting during 2010 and 2012. In the Bloemfontein area no bolting was recorded, while other areas (Pretoria, Tarlton, Dlemas, Bapsfontein, Alberton, Petrusburg, Greytown and Natal Midlands) showed bolting. Appendices A1, A2, A3 and A4 present temperatures for Bloemfontein, Greytown and Pretoria for the 2010, 2011 and 2012 production years.

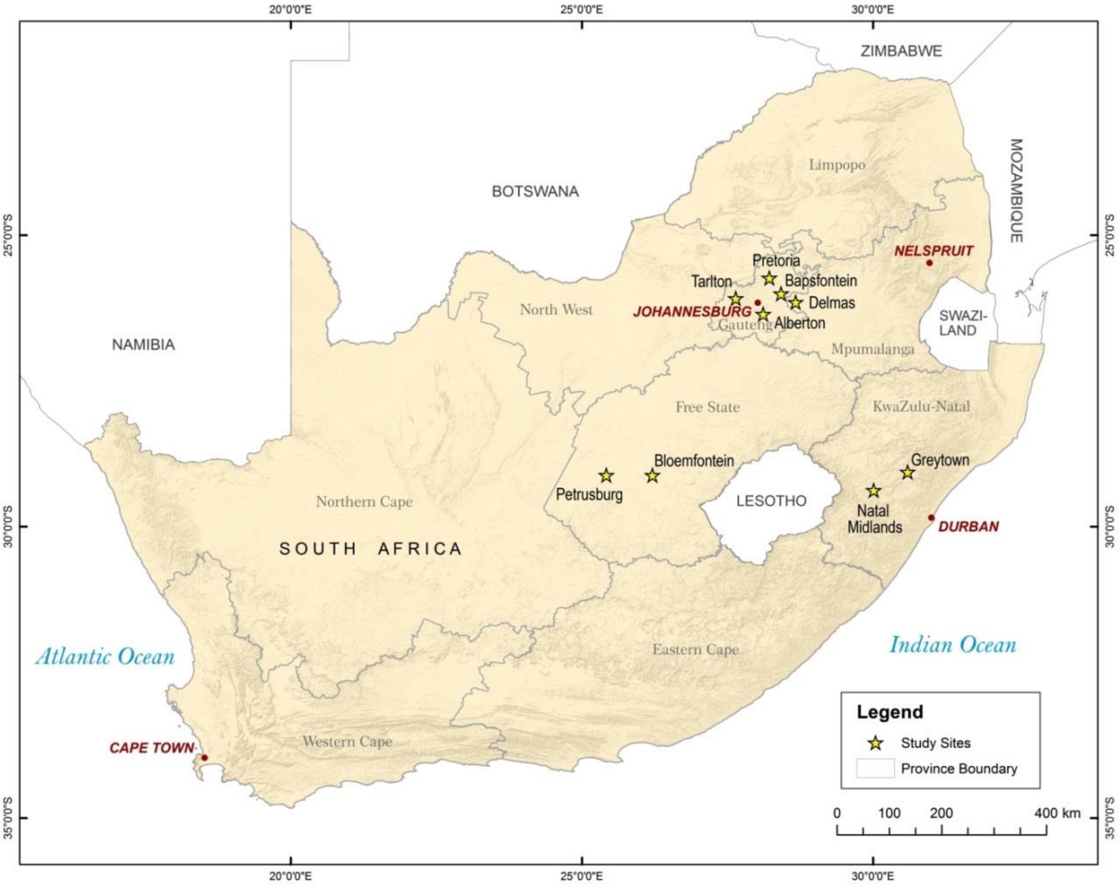


FIG i: Map of South Africa showing study sites for this research work

CHAPTER 1

LITERATURE REVIEW

1.1 Introduction

Cabbage production in South Africa and the rest of Africa is of great importance in feeding the nations and contributing in the fight against malnutrition. The promotion for an increase in vegetable consumption and the change to a better life style seems to support the necessity for increasing cabbage production (Modi *et al.* 2006). Producing sufficient cabbages for both local consumption and export is of utmost importance.

Information on growth and development of plants (Strandberg, 1979) plays an important role in understanding the factors that can impair yield. These factors have the potential of severely reducing the agricultural value of the plants (Yoshida *et al.*, 2010). Such factors include temperature, agronomic practices, phyto-hormones and photoperiod and biotic factors.

1.2 Cabbage head formation and bolting

Cabbage, as a biennial plant, forms very short internodes, and has a basal rosette of clasping leaves which, with maturity, comprise the solid storage head (Pelofske & Baggett, 1978). In early developmental stages, the cabbage plant shows no tendency to head, but as leaves become larger and growth accelerates, internodes do not elongate, new leaves arising from the apical meristem curve and cup inward, become crumpled and densely packed and overlap to cover the growing point. Head size develops slowly at first, accelerating during mid- to late growth until the head constitutes over one-half of the plant’s total weight at harvest (Pierce, 1987).

The head formation period ends with the attainment of the desired head density for harvesting. If the head is not harvested in time, further expansion of the inner leaves, and resumption of the stem elongation result in the splitting of the head. Stem extension may occur even if the plant has not received sufficient low temperature to bring about flower initiation, and seems to be part of the periodic growth cycle of the plant. Cabbage plants allowed to grow in an environment that does not induce flowering will show periodic stem extension followed by head formation. Figure 1.1

depicts a cabbage plant that produced a series of four heads (growing on points N, O, P and Q) on an elongating stalk over a two year growing period (Wien, 1997).

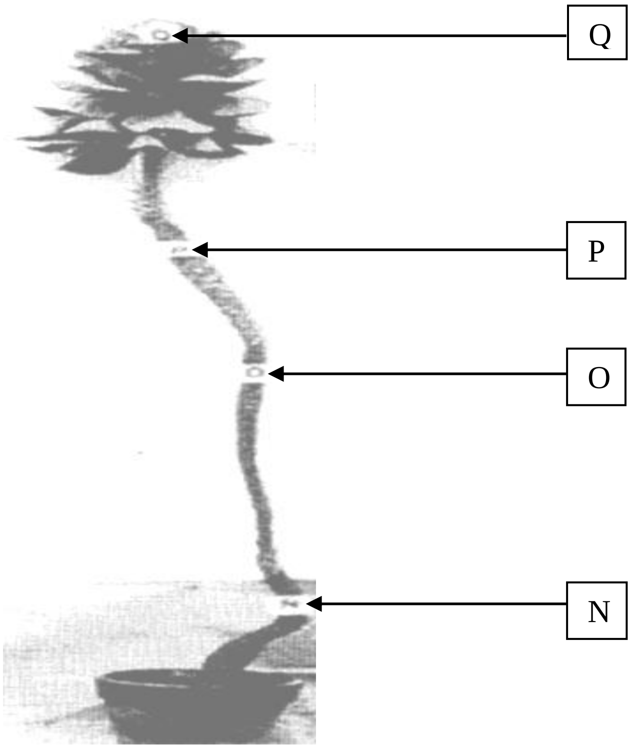


FIG 1.1 'Danish Ballhead' cabbage after two years' growth in a greenhouse at 19°C. During this time, the plant produced four heads at growing points N, O, P and Q (Wien, 1997)

1.3 Plant vernalization

Lin *et al.* (2005) stated that vernalization is a natural adaptation ensuring that flowering occurs only after winter in order for flowers and seeds to develop under favourable conditions. Wilkins (1984) and Leopold (1964) also stated that vernalization is the promotive effect of low temperatures on flowering. Chouard (1960) as cited by Michaels & Amasino (2000) defined vernalization as "the acquisition or acceleration of the ability to flower by a chilling treatment." Thus a vernalizing low temperature treatment does not initiate flower primordia directly, but creates the capacity for subsequent flowering. Vernalization is essentially a cold requirement that induces cells, in either the floral apex or those plant parts from which it would develop, so that they can flower when conditions are correct for floral development and seeding (Bidwell, 1979). Many species are induced or promoted to flower by low temperatures, especially many biennial and perennial plants. Germination in late summer would not lead to immediate flowering in favourable photoperiods, and vernalization becomes a means to ensure that winter has passed before the onset of reproduction in temperature sensitive plants (Wilkins, 1984). The vernalization stimulus is perceived normally by the apical meristem and most plant physiologists concur that the apical meristem is in fact the locus of the vernalization stimuli (Leopold, 1964).

Most of the biennial vegetables initiate reproductive growth after extended (several weeks or months) exposure to low temperature and/or a specific day length. This stimulus is more effective as plants reach the adult phase; seedlings and transplants are minimally sensitive. Induction of flowering in sensitive plants is a quantitative response to low temperature; the duration of exposure needed to initiate reproductive growth declines as the temperature declines to a certain limit. Temperatures less than 0°C do not readily fulfil the cold requirement. It is also possible to devernalize (reverse the direction of differentiation) by exposing partially vernalized plants to high temperature (Pierce, 1987). Vernalization can be reversed in its early stages by heat treatment (Bidwell, 1979).

The vernalization process requires aerobic conditions because it does not take place when plants or seeds are cooled in an atmosphere of nitrogen. Vernalization is a cumulative process as the flowering response increases with duration of cold exposure until the response is 'saturated'; it varies widely between species and cultivars within one species (< 10 to > 100 days). Once vernalization reaches its 'saturation' point, de-vernalization becomes more difficult. Although some biennial plants can be vernalized as seeds, most of them must reach a certain size before the cold treatment is effective (Wilkins, 1984).

Lin *et al.* (2005) stated that vernalization in plants can be categorized into two types according to the plant growth phase that senses cold temperature. One type is the 'seed-vernalization responsive' type, in which plants can sense cold temperatures during seed germination. The other type is the 'plant-vernalization responsive' type, in which plants need to reach a definite developmental growth stage before becoming sensitive to cold temperatures. Biennial plants that grow vegetatively in the first year and flower in the following year after winter usually belong to the plant-vernalization responsive type. Another type of vernalization is the 'facultative or quantitative vernalization requirement which refers to plants that does not require cold treatment to be vernalized but the cold treatment improves flowering characteristics such as reduced time to flower. Michaels & Amasino (2000) reported that in annual plants, low temperature exposure is not essential for flowering, but flowering will be induced more rapidly after low temperature treatment.

1.4 Timing of flowering in plants

Temperature can be considered as an ecological co-ordination of flowering times. Environmental cues serve principally to synchronize the timing of the flowering events (Leopold, 1964). It would not be appropriate for a plant to flower before it has developed sufficient leaves and roots to support fruit development (Bidwell, 1979). As an individual plant becomes older and larger, its innate tendencies to flower become increasingly forceful (Leopold, 1964). It would be decidedly disadvantageous for a plant to flower so late in the season that the fruit and seed development could not be completely developed before the onset of winter. These concepts illustrate the importance of the correlation of events into a proper sequence so that development is an orderly and not a haphazard process (Bidwell, 1979).

The two most important timing mechanisms for flowering both measure the progress of the season. One is photoperiod, a mechanism that enables plants to respond to day length so that they flower at a specific time of the year. The other is cold requirement that cold sensitive plants would not flower without it. The genetic programme for flowering is present in the cells of the apical meristem(s) but it is not expressed until “the right time” which includes the age of the plant (Bidwell, 1979).

Shoemaker (1947) reported that if cabbages are sown in autumn and grown through winter, they may bolt before the plants head. Sowing plants in autumn at relatively low temperatures is associated with bolting.

1.5 The transition to flowering in plants

Lin *et al.* (2005) reported that the transition from the vegetative to the reproductive phase is essential for the completion of the life cycle of flowering plants. Therefore, proper timing of this transition is essential for the successful completion of the reproduction process, although some plants have evolved mechanisms to control flowering time in response to environmental factors and thus co-ordinate flowering during different seasons. The timing of the reproductive transition is dependent on the developmental phase of plants and environmental conditions. A combination of these two factors ensures that flowering occurs at appropriate times with an accumulation of sufficient nutrients and favourable environmental conditions. Genetic analysis has revealed that multiple pathways, such as the photoperiod and the autonomous pathway, are involved in regulating this transition.

The transition to flowering can be broken down into two distinct processes, namely induction and evocation. Floral induction is a signal sent to the apical meristem(s), committing the plant to start producing flowers, which often happens as a result of processes occurring in the leaves. Once induced, a plant is set on the path to flowering, even though no flowers have yet been produced. The induced plant then evokes the production of flowers by triggering changes in gene expression in the apical meristem. It is clear from this physical separation of processes that floral evocation requires the production of a signal by the induced organs, which is transported to the apical meristem and activates flower production (Glover, 2007).

Glover (2007) and Lin *et al*. (2005) stated that the variables that interact to determine when a plant is ready to be induced to flower can include developmental stimuli and environmental stimuli. The developmental factors which may influence the floral transition generally refer to the age and health of the plant (Glover, 2007). The transition to the reproductive phase results in the completion of the plant's life or a growth cycle or module.

1.6 Development of floral buds and flowering

According to Daly & Tomkins (1995), the floral buds which develop, as bolting in cabbage progresses, may occur after the true head begins to form. If buds differentiate before heading begins, loose and unmarketable heads result, but heads will still form if the plant has developed a sufficient number of leaves.

The process of floral bud formation involves a complete alteration of the products of developing meristems, usually terminating the formation of leaves and internodes and imposing instead the formation of flowers and associated appendages. Flowering may be regulated by the termination of the juvenile phase of development such as cutting open cabbage heads to initiate floral development for seed production. Environmental cues may provoke the induction of the reproductive state in leaves, the initiation of floral meristems, the morphological development of flowers, or anthesis itself (Leopold, 1964).

1.7 Bolting in cabbage plants

According to Kemble *et al.* (1999), bolting is the process in which the cabbage plant switches from vegetative growth (heading) to reproductive growth (the formation of flowers and seeds). More appropriately, bolting is the term used for premature flowering in vegetables and other plants. Hebrard *et al.* (2013) also defined bolting of plants as the rapid-elongation of stems linked to the use of stored sucrose and is usually followed by the development of inflorescence, while Daly & Tomkins (1995) reported that many growers refer to bolting as being a state of advanced flower stalk development, generally at the particular point where the cabbage head becomes unmarketable (Kemble *et al.*, 1999). In fact, the process of bolting is synonymous with inflorescence initiation and development. As the cabbage stem continues to grow, it thickens, apical dominance is lost and the axillary buds develop into a number of secondary shoots within the head of the cabbage, each shoot eventually developing floral buds. Advanced bolting results in a well-developed inflorescence stalk, which penetrates through the top of the head causing distortion and cracking of the head.

As mentioned previously, bolting is initiated by a period of exposure to cold temperature (Daly & Tomkins, 1995), day length, or a combination of the two (Johnson, 2011). Plants bolt prematurely because they are exposed to cool temperatures during some stage of their development. The amount and length of cold needed depends on the species and variety (Johnson, 2011). As soon as the weather warms up, the plants bolt quickly, with the goal of producing as many seeds as possible. Gardeners typically notice bolting in the first warm spell of the year, as their plants suddenly put out flower shoots which may grow at a rapid rate (Smith, 2011). Therefore, it becomes a concern if cabbage production is extended into warmer months (Daly & Tomkins, 1995).

Hebrard *et al.* (2013) reported that a number of parameters are used to measure the bolting tolerance, such as the bolting index (BI) defined as the percentage of bolting plants, and the bolting delay (BD) which is defined as the average number of days required for a visible bolting initiation during induction.

Lin *et al.* (2005) stated that cabbage normally requires about six to eight weeks of low temperatures (5 °C) to induce bolting at the stage of seven to nine leaves and when the stem diameter reaches about 6 mm. Lin *et al.* (2005), as supported by Michael & Amasino (2000), reported that in plants where flowering is promoted by low temperature, the range of inducing temperatures is usually 1 to 7 °C, with a duration of cold of about one to three months. An inconsistency of inducing temperatures (warm temperature breaks) can affect the effectiveness of the cold treatment.

1.8 Cultivar effect on bolting

According to Shoemaker (1947), cabbage cultivars that produce small, uniform and compact heads, are less likely to bolt than those that are somewhat open-headed, leafy, and less late maturing. Cold-sensitive cultivars grown for summer production require higher temperatures to prevent premature bolting than cold-tolerant cultivars. Temperatures above 15 °C reduced bolting close to 0 % for cold tolerant cultivars, whereas all cold sensitive plants bolted at 21 °C (Daly & Tomkins, 1995). Clark & Wittwer (1949) stated that the commonly employed attempts towards the control of bolting in vegetables are through using cultivars resistant to bolting and manipulating planting dates and other cultural practices which may include fertilizer application and irrigation.

There are large differences in juvenility within cultivars and species and it may be that sensitivity to induction decreases and then increases as plants get older. After the plants have reached the adult vegetative stage, cold treatments will reduce the rate at which plants grow (Wien, 1997).

Ways of maximizing yield have over the years been exploited by scientists. Wien (1997), for example, reported that the first step towards maximizing yield by breeding is to assure that the phenology of the crop is well matched to the target environment. Matching phenology with the environment may be achieved either by genetically modifying the crop through manipulation of photoperiod or vernalization of sensitive/insensitive genes or by modifying management. This has shown to have a major influence in controlling bolting which is one of the major physiological disorders that has affected vegetable production over the years.

1.9 Plant's response to photoperiod

In flowering plants, two phases of plant growth exist. These are the juvenile and adult phases. Some people recognise a transition phase between the two phases. The transition from juvenile (vegetative) to adult (reproductive) phase of development is an essential phase in plant production. There are several factors that regulate the transition phase which include environmental conditions and endogenous signals (Kim *et al.*, 2007). Ali *et al.* (2009), Lefsud *et al.* (2006), and Lange *et al.* (1981) stated that photoperiod influences plant physiological conditions such as biomass production, intervenial chlorosis, chlorophyll, necrosis, changes in secondary compounds, bud formation, flowering, germination, leaf elongation, leaf emergence, internode length, stem height and leaf shape. Photoperiod also influences tuber formation, concentration of metabolites and growth regulators. Yui & Yoshikawa (1991) stated that flower bud differentiation and bolting in some plants are promoted by both temperature and day length. However, Chinese cabbage (*Brassica rapa* L. subs. *Chinensis*) may flower without any chilling treatment which makes photoperiod to be an important factor in its reproduction.

According to Wien (1997), environments where the day-lengths are longer than the critical photoperiod (the specific photoperiod for a specific plant to develop from the juvenile to the adult stage) delay flowering. If the photoperiod is increased sufficiently in short day plants, it ultimately reaches a value beyond which there is no further delay in flowering. Similarly, in long day plants, if day-length is decreased sufficiently, there comes a point below which there is no further delay in flowering. In each case, this is referred to as the ceiling photoperiod. Beyond this limit, the rate of progress towards flowering is unaffected by either photoperiod or temperature. Photoperiodic response to some plants can be described as obligate, since photoperiods less than ceiling photoperiods in short day plants, or greater than ceiling photoperiods in long day plants are an obligate requirement if the plant is to remain vegetative.

Clark & Wittwer (1949) reported that the interest in bolting goes beyond the field of crop production and extends into the realm of the fundamental study of plant development.

Photoperiod is one of the most important factors in flowering and, hence bolting (Fife & Price, 1953). Plants which are induced to bolt during seed germination are mostly induced by photoperiod. Burn *et al*. (1993) mentioned in their report that some plants require short days, while others require long days to initiate flowering. The site of perception for day-length is the leaf, where a signal is formed and successively translated to the shoot apex, where a new pattern of cell division forms flowering meristems that subsequently produces the inflorescences.

According to Pressman & Aviram (1986), photoperiod enhance the effect of vernalization in plants and increases the rate of bolting after vernalization. Michaels & Amasino (2000) also reported that there are at least four pathways that promote flowering in *Arabidopsis*: a photoperiod pathway, a GA-dependant pathway, an autonomous or constitutive pathway and a vernalization pathway (Figure 1.2).

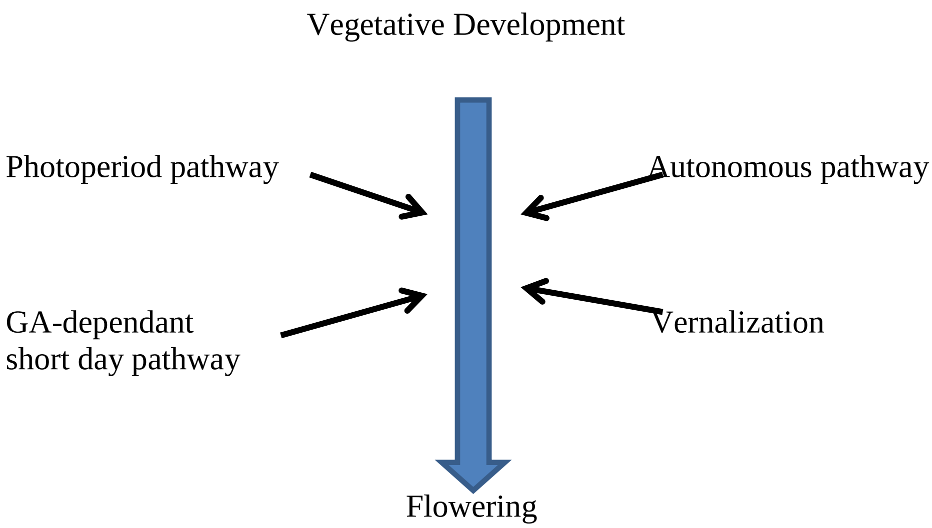


FIG 1.2: Four pathways that promote flowering in *Arabidopsis* (Michaels & Amasino, 2000)

1.10 Cabbage acclimatisation to cold temperatures

Plants are generally said to be poikilothermic organisms as they are usually not adapted to control their own temperatures by producing heat. Therefore, for plants to avoid general severe environmental stresses such as low temperature, cold-tolerant plants usually use a number of physiological and metabolic responses that lead to cold acclimatisation. It has been discovered that there are other plants called “thermogenic plants” that activate specific metabolic pathways to increase the temperature of a particular organ or tissue (Ito *et al.*, 2004).

Cox & Levitt (1975) found that low, but non-freezing temperatures (0-10 °C) induce freezing resistance in plants that have hardening capabilities. Drought-hardening induced maximum freezing tolerance in cabbage leaves fully equal to that obtained by low temperature hardening.

Leafy plants from temperate regions generally tolerate low temperatures below -5 °C and this depends on the species affected. Most importantly, the maximum freezing tolerance of plants is not “constitutive”, but is induced in response to low, non-freezing temperatures (below approximately 10 °C). Low temperatures have been found to periodically lead to significant losses in plant productivity and yield and thus, limit the geographical locations where crop and horticultural plant species can be produced (Thomashow, 1998).

Conclusions

Cabbage vernalization comes about by the exposure of plants to cold temperatures: however, low temperature exposure does not initiate bolting but induces it. Cabbage plants initiate reproductive growth after exposure to low temperatures of about 5 °C for at least six weeks at a specific photoperiod. Cabbage responds to vernalizing temperatures after reaching a definite developmental growth stage. After vernalization, floral buds may develop after the true head development has been completed. The stage of head development at the time of bolting initiation will determine the marketability of the heads. In the literature, there is a lack of reference to stage of plant development at the time of exposure to low temperatures.

CHAPTER 2

LOW TEMPERATURE EFFECTS ON CABBAGE SEEDLINGS

2.1 Introduction

Juvenility is the term normally given to the early phase of plant growth during which flowering cannot be initiated under inducive conditions. In many plants, the transition to flowering occurs after the juvenile phase has been completed without any exposure to any particular stimulus. The juvenile phase in most herbaceous plants is usually quite short. Juvenility is important, as it appears to be a device to ensure that flowering does not occur until a plant is large enough to support the energetic demands of seed production (Wilkins, 1984).

In the commercial cabbage production, seedlings are used for establishment. It is essential that, when high yield and quality of the final products is to be obtained, seedlings should be adapted and prepared for field production (Kalisz & Siwek, 2006). Cabbage is a biennial winter crop and early planting in autumn is crucial to allow an early harvest and, consequently, a high price; however, there is a risk of environmental stress associated with exposing young plants to cool weather. For this reason, it is ideally important to prepare plants for outdoor conditions. One of the used techniques for plant acclimation is exposing plants to lower temperatures before planting. Proper manipulation of this factor during the period of cabbage seedling propagation in a greenhouse supposedly leads to an increase in tolerance to bolting during adverse field conditions during the winter season (Kalisz & Cebula, 2006).

The response of plants exposed to unfavourable temperatures is a result of modifications of many physiological and biochemical processes leading to changes in the chemical composition in the plant (Kalisz & Cebula, 2006). In cabbage production, planting date can influence yield components, like sugar levels and fresh cabbage flavour, which may be due to the formation of inflorescence primordia inside the cabbage head (Radovich *et al.*, 2005). The degree of these changes mainly depends on temperature level, temperature exposure duration and the stage of plant development. Seedlings are generally more sensitive to unfavourable thermal conditions than more developed plants (Kalisz & Cebula, 2006). The effect of low temperatures prevailing at early stages of plant growth is associated with premature flowering (Kalisz & Siwek, 2006). Therefore, low air temperatures during hardening of transplants may bring about an increase in the percentage of bolting plants (Kalisz & Cebula, 2001). Floral development can also be advanced by temperatures above 12 °C (Guttormsen, 1981).

According to George (1985) flowering can also be affected by plant age and leaf number which are important in the plant's receptiveness to low temperatures. Many seedlings, about 2.5 to 3.75 cm wide (seen from the top) at transplanting, will bolt, if exposed to continuous 5 °C vernalizing temperatures for a period of 30 to 60 days (Guttormsen, 1981). The size of the plant at the time it is exposed to low temperatures is therefore of considerable importance. Thompson & Kelly (1959) mentioned that, the larger plants (after transplanting) are at the time of low temperatures, the greater the tendency for over-wintered cabbage to bolt in spring (Thompson & Kelly, 1959). Research conducted by Guttormsen (1981), showed that three-week-old cabbage transplants are less susceptible to bolting than one-week-old transplants when subsequently exposed to vernalizing temperatures. It was found that transplants should receive a certain number of leaves to be able to bolt.

The longer the period of cold exposure results in higher percentage of plants producing inflorescences. Freezing temperatures that bring about premature flowering, but low growing temperatures (0 °C) initiate bolting (Ware & McCollum, 1980).

From the review above, it is clear that the results obtained by different authors are not providing specific information on temperature effect on cabbage bolting it was therefore decided to test the sensitivity of seedlings under local conditions.

The aim of this experiment was to determine whether bolting could be induced by exposing cabbage seedlings to different night temperatures prior to planting as well as to determine the general effect of the cold treatments on cabbage growth and heading.

2.2 Materials and Methods

Two cabbage cultivars, 'Conquistador' (a cultivar highly resistant to bolting) and 'Grandslam' (a cultivar highly susceptible to bolting), were used for this experiment. The characteristics of the cultivars are summarised in Table 2.1 and the recommended planting dates in Table 2.2

Table 2.1: Agronomic description of 'Conquistador' and 'Grandslam' cultivars

Cultivar	Days to harvest	Head mass(kg)	Head shape	Bolting reaction
'Conquistador'	90 – 120	3 – 4	Thick flat	Heat and cold tolerant
'Grandslam'	90 – 110	3 – 5	Round	Sensitive to bolting

(Extracted from Sakata Seed Southern Africa, 2014)

Table 2.2: Recommended planting times for 'Grandslam' and 'Conquistador' in the Gauteng Province

Cultivar	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
'Conquistador'	■	■						■	■	■	■	■
'Grandslam'	■	■										

(Extracted from Sakata Seed Southern Africa, 2014)

The experiment was conducted at the Experimental Farm and the Plant Science Complex of the University of Pretoria. Two growth chambers allowing temperature and light (control simulating local day and night conditions) were used, providing a temperature range of 10 °C to 30 °C and an average photosynthetic active radiation (PAR) of 361.57 $\mu mol \cdot m^2 \cdot s^{-1}$. The chambers also had about 90% relative humidity. A separate cold room for the 4 °C night temperature treatment was used. Seeds of the two cultivars were sown (Table 2.3) and grown in the commercial growing medium, 'Hydro-mix', and raised in a glasshouse for one week at ambient temperature. After emergence, a mixture of calcium nitrate (15.5% nitrogen and 26.5% calcium) (3.2 g/5 L), K-max 0-0-14.5 (14.5% potassium) (5 ml/50 L) and Hydro-grow (micro nutrients), a commercial fertilising mixture (5 g/5 L) were used to fertilize the seedlings until transplanting. Two weeks after sowing, the seedlings were exposed to the treatments as indicated in Table 2.3 for a period of three weeks.

Table 2.3: Treatment of cabbage seedlings three weeks prior to transplanting

Treatment Number	Night temperatures (8 hours in the dark)			Day temperatures (16 hours of photoperiod)	Ambient temperature (18 minimum and 23 °C maximum day temperature) and uncontrolled photoperiod
	4 °C	10 °C	15 °C	20 °C	
1	X			X	
2		X		X	
3			X	X	
4					X

After the cold treatments, the seedlings were taken to a glasshouse at ambient day temperature (18 °C minimum and 23 °C maximum) for hardening-off for a period of ten days before they were transplanted in an open field at the University of Pretoria's Experimental Farm.

A 2:3:4 (38%) fertilizer was applied at 600 kg/ha during transplanting as a basal fertilizer and limestone ammonium nitrate (LAN, 28%) at 300 kg/ha as topdressing five weeks after transplanting. The plants were watered using over-head sprinklers twice a week, depending on weather conditions and plant requirements.

Harvesting was carried out three months (110 days) after transplanting (Table 2.4). During harvesting, the following growth parameters were recorded: Head mass with and without cover leaves, vertical (axial) and horizontal (transverse) head diameters, core length and diameter and dry mass of the cabbage head without basal leaves.

Table 2.4: Experimental activity plan/time table

Activity	Date
Sowing	18 January 2012
Treatments	30 January to 17 February 2012 (3 weeks)
Hardening-off	17 February to 28 February
Transplanting	28 February 2012
Harvesting	19 June 2012

Figure 2.1 shows the average weekly temperatures for the first week of March to the third week of June 2012, recorded during the experiment. Plants were planted when the average maximum temperatures were high (about 25 °C) with an average minimum temperature of 17 °C in March. The minimum temperatures started to drop from April and reached a minimum of 4 °C in June.

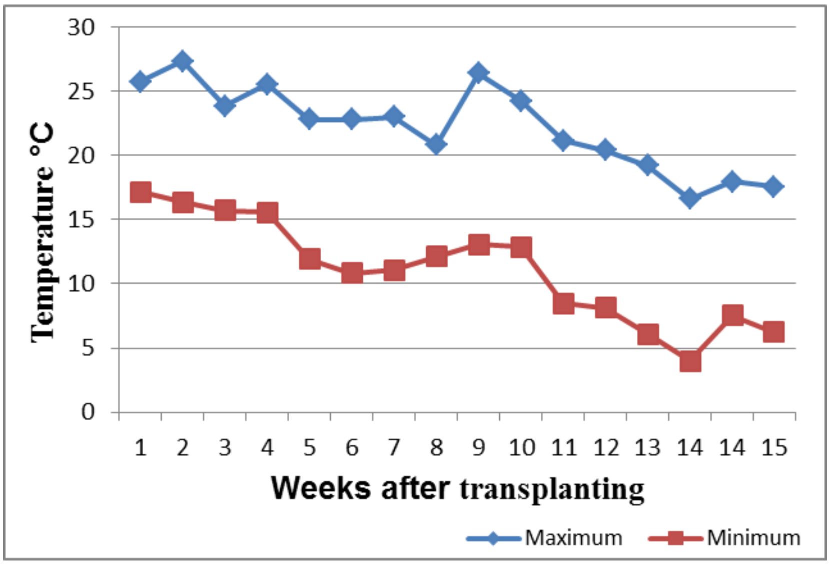


FIG. 2.1: Average maximum and minimum weekly temperatures for the months from the first week of March to June 2012 recorded at the weather station at the University of Pretoria Experimental Farm close to the open field experimental site

2.3 Results and Discussion

2.3.1 Temperature effects on plant growth

The two cultivars, 'Conquistador' and 'Grandslam', showed differences in growth rate and plant size during the cold temperature treatment. Figure 2.2 shows that 'Conquistador' seedlings had longer internodes than those of 'Grandslam' irrespective of the environmental growing conditions. The differences between the two cultivars were due to genetic differences. Figure 2.3 shows a healthy transplant growing in the open field after treatment at 4 °C.

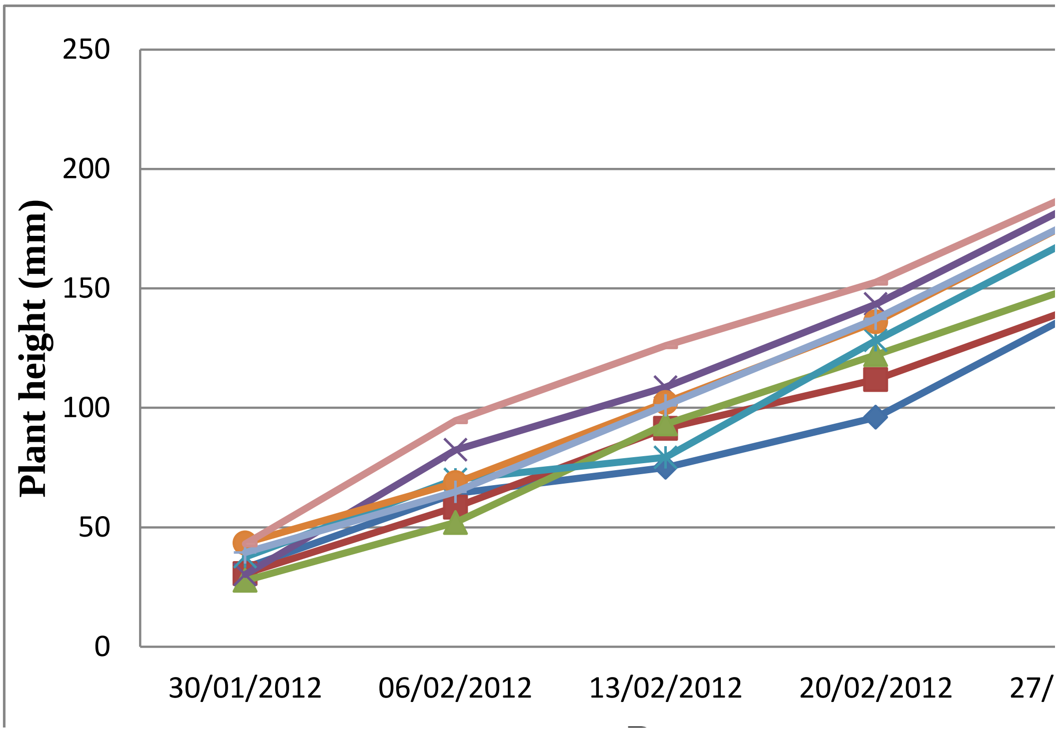


FIG. 2.2: 'Conquistador' (CO) and 'Grandslam' (GR) seedling growth rate for the five week period from treatment to transplanting. Night temperature treatments: A1- 4 °C, C1- 10 °C, P1- 15 °C and D1- ambient

FIG. 2.3: A nine-week old 'Grandslam' cabbage (4 °C treatment) plant growing in the open field

There was no significant difference between the mass of the cabbage heads with and without wrapper leaves for the four treatments (Table 2.5). Thus suggesting that low temperatures did not have any major effect on cabbage yield, however, there was a growth lag phase when plants were exposed to low temperatures. Therefore, cabbages plants showed the potential of negating the effects of low temperature received during the seedling stage when they were subsequently grown at temperatures or environments conducive to bolting in the open field. All the treatments produced good head size regardless of the cultivar harvested. The reasons for this finding should be seen in greater acclimation ability to field conditions of hybrid plants exposed to lower temperatures prior to transplanting.

Table 2.5: 'Grandslam' and 'Conquistador' head average fresh mass

Treatment temperature °C	**Mean mass with wrapper leaves (kg)**	**Mean mass without wrapper leaves (kg)**
4	5.1718[a]	3.5063 [a]
10	5.2202 [a]	3.6058 [a]
15	5.3897 [a]	3.6957 [a]
Ambient	5.1503 [a]	3.5090 [a]

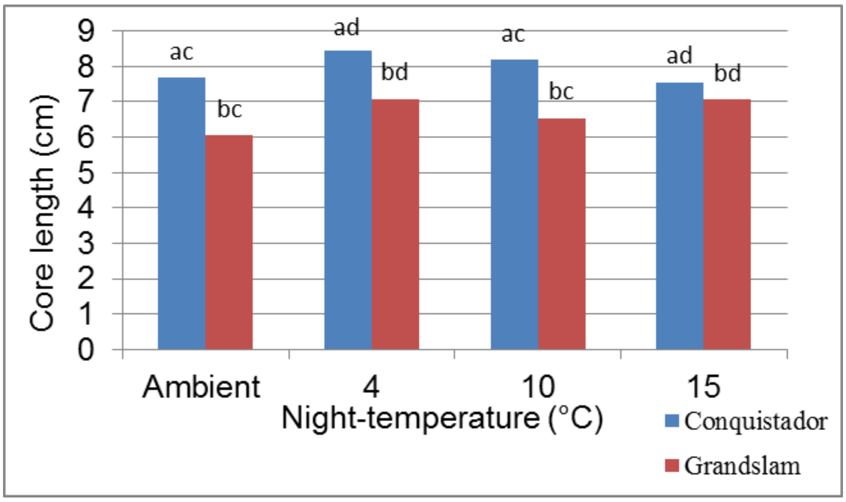
NB: Means with the same letter are not significantly different.

2.3.2 Transition of plants from vegetative to reproductive structures

Cabbage seedlings subjected to the cold pre-treatments were not induced to bolting and, thus, the plants did not show any signs of bolting in the field. Up until harvesting there was no visible bolting (Figure 2.4). The core length was short compared with the cabbage plant (Figure 2.5). There was a significant difference in the core length of the cabbage cultivars (Figure 2.6). 'Grandslam' had a shorter core length than 'Conquistador', consistent with the cultivar description. 'Conquistador' had 8.18 cm core length, compared to 6.52 cm for 'Grandslam' for the 10 °C night temperatures. The difference in core length was consistent with the other three treatments, however, ambient and the 10 °C treatments were significantly different to 4 °C and 15 °C treatments. This difference does not have a link with the effect of temperature on bolting. Thus, the observed differences were probably due to genetic variation not to temperature effect. Core length was used as a tool to identify, if there was any core elongation as a result of temperature effects which could have been a sign of bolting.

FIG. 2.4: 'Grandslam' cabbage plant that was exposed to 4 °C treatment during seedling growth, before growing in the open field at ambient conditions (Fig. 2.1) showing no signs of bolting

FIG. 2.5: Split 'Grandslam' cabbage head that was exposed to 4 °C before planting and grown in the open field for 110 days. All the cabbages from the different treatments resembled similar head attributes



NB: Means with the same letter are not significantly different. 'a' and 'b' represent significant difference between cultivars and, 'c' and 'd' represent significant difference between treatments.

FIG. 2.6: Length of cabbage head core in the two cabbage cultivars: 'Conquistador' and 'Grandslam' after exposure to ambient, 4, 10 and 15 °C treatments.

The reason for the non-bolting of the plants could have been that the seedlings were still young and the duration of the low temperature did not stimulate the seedlings to reach a saturated vernalization point (point of no return) according to Wilkins (1984). Thompson & Kelly (1959) showed that the size of the plant at the time it is exposed to low temperatures is of utmost importance. That is, the larger the plants are at the time of exposure to low temperatures, the greater is the tendency for the over-wintered cabbage to bolt when temperatures get warmer. Only after Week 5 that average weekly minimum temperature in the open field dropped below 15 °C and after Week 11 it dropped below 10 °C (Figure 2.1); the temperatures were conducive for bolting. This confirms the finding of Lin *et al.* (2005), who stated that flowering is promoted by temperatures ranging from 1 to 7 °C. This means that the plants were exposed to conducive conditions at two different growth stages (seedling and heading stages) but none of these temperatures induced bolting. The possible reasons for the plants not undergoing bolting could have been that these cultivars used cannot be induced to bolt during the seedling stage as confirmed by Thomas (1980), who reported that plants cannot be induced until they have outgrown the juvenile phase.

2.4 Conclusions

This experiment has demonstrated that growth of both, ‘Conquistador’ and ‘Grandslam’ cabbage is influenced by temperature, especially at the younger stages of growth when the plants were exposed to varying low temperatures: however, after being exposed to open field conditions, the initial temperatures did not affect the growth and development of the cabbages. This shows that cabbage plants can adjust to different temperatures as long as they are not exposed to severe cold temperatures which can damage the plants.

The experiment has also shown that bolting cannot be induced during the seedling stage of hybrid cabbages, as there were no signs of bolting during the growth of the cabbages. The age of the seedlings during the temperature treatment could have been the major controlling factor for the receptiveness of the plants to low temperature.

2. 5 Recommendations

A further study on the response of cabbage plants to the effect of temperature needs to be undertaken in order to ascertain and identify critical information on the effects of temperature on cabbages.

CHAPTER 3

RESPONSE OF CABBAGE TRANSPLANTS TO CONTROLLED LOW TEMPERATURES

3.1 Introduction

Bolting in a cabbage crop may mean a total loss to the farmer. Cabbage plants grow and respond differently to temperatures to which they are exposed to. Adeniji *et al.* (2010) reported that the optimum average temperature range for early growth is 18 to 20 °C, 15 to 16 °C for early head development, and 10 to 13 °C for final head development, while Salunkhe & Kadam (1998) stated that the general optimum temperature for cabbage growth is 15 to 20 °C. When temperatures are below 0 °C, growth is stopped. Kemble *et al.* (1999) reported ranges from 15 to 18 °C to be optimal for cabbage growth and development.

A cabbage plant exposed to 10 to 13 °C for several months after transplanting will initiate bolting and two weeks of exposure to temperatures of 13 °C or lower also induce bolting, but this process will only be initiated when the chilling requirement is met (Daly & Tomkins, 1995). The percentage bolting will increase with increasing exposure to temperatures at or below 4.4 °C. If the plant is then exposed to a 2 °C environment, inflorescences will emerge rapidly, splitting the centre of the head (Pierce, 1987). High altitude, cold climate, great variations in temperature and long day length produce small heads and high rates of bolting before maturity (WuFeng & SunKai, 1995). A vernalization temperature range of 3 to 7 °C can be suitable for most cabbage cultivars, but strong winter plants can exhibit optimum flower bud differentiation and bolting even at 11 °C (MaiXia *et al.*, 2004). An increase in day temperature does not nullify the vernalizing effect of low night temperatures, but delays bolting. Cold sensitive cultivars exposed to temperatures of 24 °C for up to three weeks prior to chilling temperatures of 15 °C for one week, can bolt (Daly & Tomkins, 1995).

Silva *et al.* (1982) stated that in temperate areas, cabbage grows vegetatively after sowing and switches to the reproductive phase after exposure to low autumn and/or winter temperatures. According to Kumar *et al.* (2009) flower differentiation in cabbage plants occurs after exposing the plants to temperatures ranging from 4 °C to

10 °C, but this depends on the developmental stage of the plant, on the cultivar and on the period of exposure to low temperatures. Tropical cabbages grown in summer in low temperature areas may produce a large number of plants with inflorescences developing within the cabbage head, which will ultimately cause the heads to burst or crack, however, not all heads that crack, bolt right-away.

Seymour & Blaylock (1999), mention that increasing growing temperatures may enable early flower development in skunk cabbages, if the plants were previously exposed to low temperatures. Once plants are growing at increased temperatures, they increase their development rate which permits early flowering.

In a research conducted by Wien (1997), flowering in cabbages was found to be delayed, but was not prevented, by the exposure of cabbages to daily temperature cycles of 16 hours at 9 °C (night), and eight hours at 27 °C (day). There was no differentiation of reproductive structures after reversing the regimes to eight hours at 9 °C during the night and 16 hours at 27 °C during the day, even after 120 days of exposure. Wien (1997) continued to mention that when cabbage plants were exposed to 9 °C for 24 hours, the plants took less than 40 days to flower. This emphasizes that long hours of exposure to low temperatures promote flowering in cabbages.

According to Shoemaker (1947), cabbage varieties that produce small, uniform and compact heads, are less likely to bolt than those varieties with somewhat open heads, leafy, and are early maturing. It is commonly accepted that average daily temperatures above 15 to 18 °C significantly reduce flower initiation and bolting as compared with lower temperatures. Exposing cabbage plants to 18 °C over a four week period is said to be sufficient to prevent premature bolting of cold tolerant cultivars exposed to subsequent day/night temperatures of 15/12 °C. Cold sensitive cultivars grown for summer production require higher temperatures to prevent bolting than cold tolerant cultivars. Average temperatures above 15 °C may reduce bolting to practically nothing for cold tolerant cultivars, whereas all cold sensitive plants bolted at 21 °C (Daly & Tomkins, 1995). Unfortunately, authors do not always mention the developmental stage of the plants subjected to the cold treatment. Determining the link between cabbage developmental stages with vernalizing temperatures could play an important role in understanding bolting and flowering in cabbage plants. Flowering is affected by the plant's age and leaf number which are important in the plant's receptiveness to low temperatures (George, 1985). The size of the plant at the time it is exposed to low temperatures is of utmost importance. The larger the plants are at the time temperatures are low, the greater the tendency for over-wintered cabbage to bolt in spring (Thompson & Kelly, 1959).

Table 3.1 lists the optimum temperatures as stated by different authors for cabbages while Table 3.2 summarizes temperatures necessary for vernalization to occur in both green cabbage and Chinese cabbage plants. The authors found similar temperature regimes for both growth and bolting.

TABLE 3.1: Suggested cabbage optimum growth temperatures

Author	**Cabbage optimum growth temperatures (°C)**
Adeniji *et al.* (2010) and Salunkhe & Kadam (1998)	15 – 20
Kemble *et al.* (1999)	15 – 18

TABLE 3.2: Suggested temperatures necessary for green cabbage and Chinese cabbage vernalization

Author	**Temperatures necessary for bolting (°C)**
Silver *et al.* (1982)	4 – 10 (cabbage)
Pierce (1987)	4 (cabbage)
Daly & Tomkins (1995)	10 – 13 (Chinese cabbage)
Maxia *et al.* (2004)	4 – 10 (Chinese cabbage)

Although cabbage is regarded as a cool season crop, extensive breeding has been done to allow cabbage to be grown all year round; however, Sakata Seeds Southern Africa (Ltd), a seed company, does not recommend all year round cabbage production for most cultivars. The period between March and July is not recommended for any planting and sowing for South African conditions, since it is part of the winter period, and bolting is highly likely, if plants are exposed to cold temperature conditions. Additionally, plants could possibly suffer stunted growth and subsequent yield loss due to poor or no head formation. Therefore, the aim of this experiment was to determine the effect of temperature on transplanted seedlings of two cabbage cultivars and also to determine whether bolting can be triggered after transplanting. Tables 2.1 and 2.2 in Chapter 2 supply details of the main characters of the cultivars to be used in this experiment.

3.2 Materials and Methods

3.2.1 Effects of low temperature applied during the cupping stage (Experiment 1)

Seedlings of two cabbage cultivars ('Conquistador' and 'Grandslam') were raised from seed at ambient temperature (13 °C night temperature and 25 °C day temperature) from the 18th of January 2012, in a glasshouse at the Experimental Farm, University of Pretoria (25° 45 N, 28° 16 E, 1372 m above sea level). Hygrotech^{R} mix was used as growing medium in 200 holes seedling trays. After six weeks (01/03/2012) from sowing (cupping stage), the seedlings were transplanted into three liter planting bags using sand and coir mixture as growing medium. The transplanted seedlings were exposed to three treatments as outlined in Table 3.3 for a period of six weeks. Two growth chambers in the Plant Science Complex at the main campus of the University of Pretoria were used for simulating of day and night conditions. The two chambers had an average photosynthetic active radiation (PAR) of 361.57 $\mu mol \cdot m^{2} \cdot s^{-1}$ measured at leaf level. They were both set at a standard 20 °C day temperature and 10 °C and 15 °C night temperature for chamber 1 and 2 respectively. The chambers were maintained at 100% relative humidity. A 4 °C cold room was used in addition to the two chambers. The plants in the 4 °C cold room were transferred to one of the chambers since it had a constant temperature and no light during the day.

TABLE 3.3: Treatments of cabbage seedlings in planting bags exposed to low temperatures during cupping stage

Treatment Number	Night temperatures (8 hours in the dark)			Day temperatures (16 hours of photoperiod)
	4 °C	10 °C	15 °C	20 °C
1	X			X
2		X		X
3			X	X

During the treatments, the cabbage plants were watered and fertilised using a mixture of liquid calcium nitrate (15.5% nitrogen and 26.5% calcium) (3.2 g/5 L), K-max (14.5% potassium) (5 ml/50 L) and 'Hydro-grow' mixture (1 g/L).

After six weeks, plants were transplanted on the 17th April 2012 into an open field plot (about 50 m away from a local weather station) until they were ready for harvesting. A 2:3:4 (38%) (600 kg/ha) complete fertilizer was incorporated into the soil before planting. Limestone ammonium nitrate (LAN, 28%) (300 kg/ha) was applied as a top-dressing on the 24th April 2012. Plots were irrigated using sprinklers and normal field management practices were applied which included manual weeding. There were two blocks with six plots each. Due to limited space in the growth chambers, the cold treatments consisted of two lines per cultivar with five plants in each line.

When the plants were ready for harvesting after four months (24 August 2012) in the field, maturity was evaluated by determining the firmness of the head by pressing the top part of the head down using thumbs. Five cabbage heads per plot were harvested and taken to the laboratory for measurements and observation. Head mass with and without wrapper (cover) leaves, circumference of the head; core length and width were measured. The heads were split in half whereafter the cut surfaces were observed for any signs of flower formation. The cabbages remaining in the field were observed for any structural or physiological changes and for bolting for about a month.

3.2.2 Effect of temperature on cabbage cultivars after the seedling stage (Experiment 2)

The experiment was started at the Plant Science Complex in the Hatfield Campus of the University of Pretoria from the 1st of March to the 26th July, 2013. Three cultivars, namely 'Conquistador', 'Grandslam' and 'Tenacity' were used for this experiment. 'Tenacity' and 'Grandslam' are known to be highly susceptible to bolting, while 'Conquistador' is a less susceptible cultivar.

Six-week-old seedlings of the three cultivars obtained from Sakata Seeds, Lanseria (26° 32S and 28° 43E) were transplanted into eight litre black planting bags. A mixture of sand and coir was used as growing medium. For each cultivar, ten plants were used for each temperature treatment. The seedlings were allowed to grow under ambient temperatures (13 °C night and 25 °C day temperatures) in a glasshouse to become well established in the planting bags in order to obtain high plant vigour and allow the transplants to reach the 'cupping' stage before exposure to low temperatures. The transplants were exposed to low temperatures for two months, from the 1st of March to the 7th of May 2013. Two plant growth chambers (walk-in types) were used. The growth chamber settings are indicated in Table 3.4.

TABLE 3.4: Temperature and photoperiod treatments of 'Conquistador', 'Grandslam' and 'Tenacity' cabbage seedlings

Growth chamber	**Day temperature**	**Night temperature**	**Light intensity (PAR)**
Growth chamber 1	20 °C for 13 hours	10 °C for 11 hours	361.57 $MJm^{-2}s^{-1}$
Growth chamber 2	15°C for 13 hours	10 °C for 11 hours	361.57 $MJm^{-2}s^{-1}$

After two months of cold treatment, the temperatures in both growth chambers were increased to 30 °C during the day and 20 °C during the night while photoperiod remaining the same. The plants were exposed to the higher temperatures from the 7th of May to the 26th of July (three months). The change in temperature was necessary for bolting to occur since low temperatures are only capable of vernalizing the plants and the transition to high temperatures was expected to trigger the plants to bolt.

After three months of high temperature exposure, cabbage plants were harvested. Cabbage heads were weighed with wrapper leaves and without wrapper leaves. The heads were then cut into halves along the stem core. The stem cores were observed for any signs of flowering which included development of inflorescence buds, and length of stalk in relation to the diameter of the head. The remaining plants (five plants per cultivar) were subsequently transferred to a 10% white shade net to allow further growth and development and observation of any physiological changes, such as heading, head shape and head cracking.

3.3 Results and Discussion

3.3.1 Experiment 1: Effects of low temperature applied during the cupping stage

3.3.1.1 Effect of low temperature on cabbage growth

Cabbage plants showed differences in growth during the cold treatment stage (Figure 3.1). Plants of ‘Conquistador’ grew much taller (stem) as compared to ‘Grandslam’ which were shorter and with broader leaves. The plants grown under 4 °C night temperature were smaller in size as compared to those under (15 °C night temperature) which was influenced by cultivars genetic make-up.

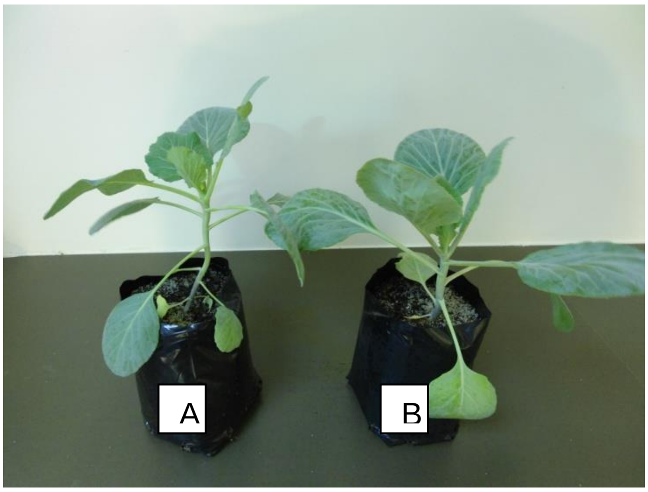


FIG. 3.1: Three week old (after transplanting) cabbage plants (A = ‘Conquistador’ and B = ‘Grandslam’) grown in growth chambers set at 15 °C (night temperature) and 20 °C (day temperature)

After transplanting the plants to the open field, up until harvesting, the plants of both cultivars and all treatments showed a similar growth pattern and growth rate irrespective of the treatment or cultivar (Figure 3.2).

FIG. 3.2: Cabbage plants in open field experimental block four weeks after transplanting

Six weeks after planting in the open field, minimum night temperatures dropped to below 10 °C while maximum day temperatures dropped below 20 °C (Figure 3.3). There low temperatures slowed the growth rate, hence these plants took much longer to reach a marketable head size. In August, week 17 and onwards (Figure 3.3), the temperatures began to warm-up which supported increased growth rate (production of leaves and head size) on the plants. The increase in growth rate caused cracking of some of the heads in all the treatments (Figure 3.4). The Manitoba Agriculture, Food and Rural Initiative (2014) reported that head cracking or splitting may be a result of well-developed heads receiving heavy rains following a prolonged period of water stress.

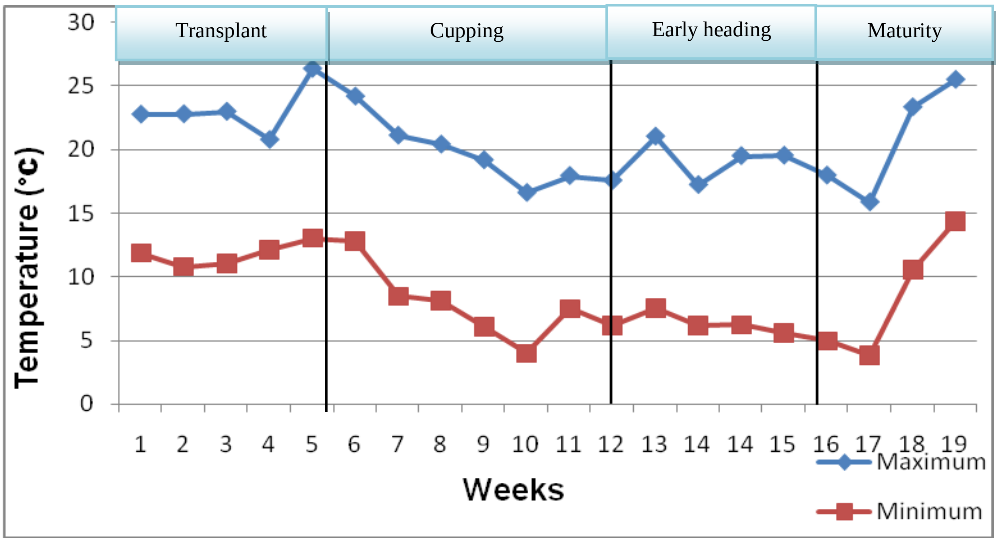


FIG. 3.3: Average maximum and minimum weekly ambient temperatures recorded at the experimental site from first week of April 2012 (Week 1) to last week of August 2012 (Week 19) in relation to growth stages

FIG. 3.4: A ‘Grandslam’ cabbage from 15 °C growth chamber forming cracks at maturity while growing in the open field

3.3.1.2. Temperature effects on cabbage bolting (Experiment 1)

The cold treatments that the plants were exposed to before transplanting were supposed to be conducive for bolting initiation. After transplanting in the open field, the day temperatures were above 20 °C for the first eight weeks (Figure 3.3) which was supposed to allow inflorescence development but none of the plants showed any external signs of bolting.

However, after the eight week growing period, the temperatures dropped below 20 °C which were therefore conducive for normal cabbage head growth as reported by Adeniji *et al.* (2010), Kemble *et al.* (1999) and Salunkhe & Kadam (1998) that 15 to 20 °C are conducive temperatures for cabbage head development. Core length did not differ between treatments (Figure 3.5) with the exception of ‘Conquistador’ exposed to 10 °C which could have been due to the increased growth rate of the core caused by head cracking which was as a result of cultivar response to change in growth patterns initiated by the sudden change in temperature in the last three weeks of growth. Statistical analysis also showed that there was no significant difference ($F > 0.05$) between core length and head mass. The trend line also shows that the treatments had approximately the same average core lengths.

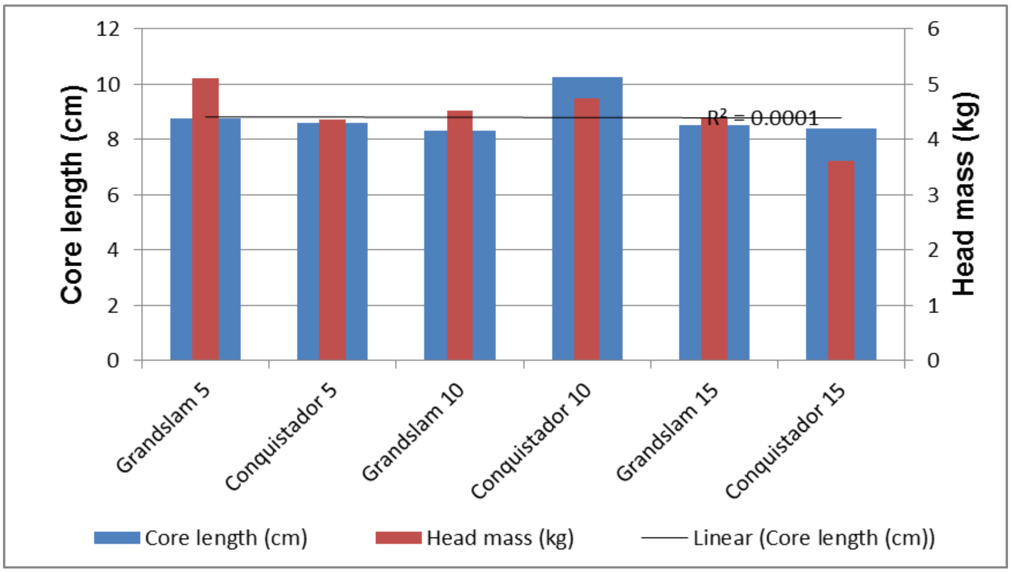


FIG. 3.5: Core length and head mass for 'Grandslam' and 'Conquistador' cultivars after three temperature treatments. There was no significant difference in the results. Trend line measure the average core length

When field minimum temperatures began to drop below 10 °C, in week eight, the plants had not shown any external signs of bolting and that subsequently prompted the plants to form heads. This is illustrated in Figure 3.6A, showing the cut surface of a firm 'Grandslam' with a short core and compacted leaves around the core. Figure 3.6B shows the cut surface of a 'Conquistador' head with no signs of bolting. It had a long core but compact leaves around the core (as also shown by Figure 3.5) which resembles a healthy and marketable cabbage head. Figure 3.7A shows a cut surface of a 'Grandslam' head section which had a compact and firm head with leaves growing upwards rather than growing in a circular (normal) way (covering the core) as shown by Figure 3.7B. This could be the first signs of bolting, although the axillary buds were still inconspicuous.

FIG. 3.6: Cut surfaces of 'Grandslam' (A) and 'Conquistador' (B) cabbage heads with no signs of bolting after pre-planting exposure to 15 °C night temperature and ambient conditions in the open field (Fig. 3.3)

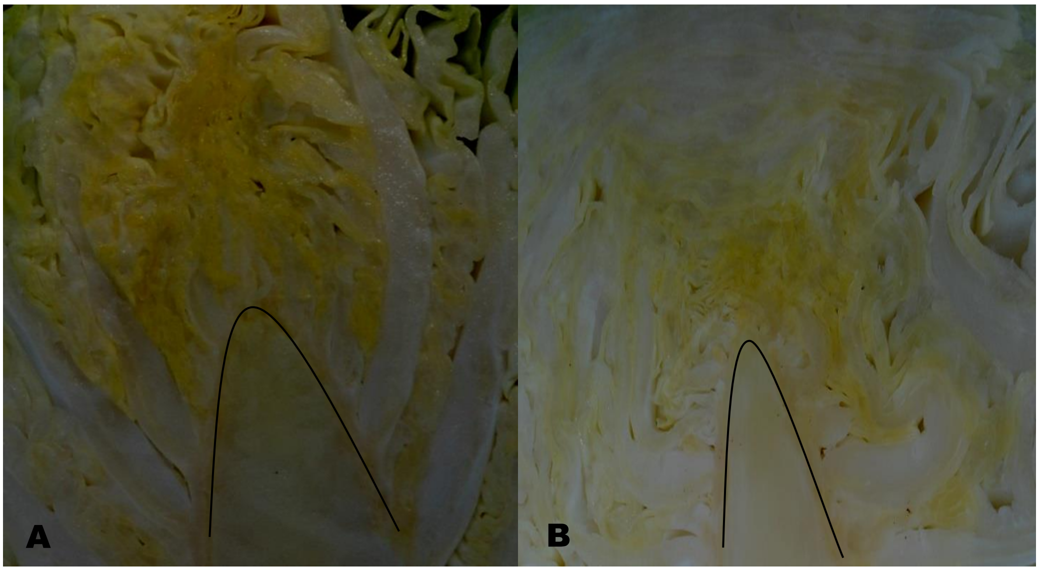


FIG. 3.7: Cut-surface sections of cabbage head (A) with elongated stalk and leaves growing towards the apex of the head and (B) growing in a circular (normal) pattern.

Plants were transplanted on the second week of April and the temperatures were sufficiently conducive for bolting after transplanting into the open field as illustrated by Figure 3.3. That was possible because the temperatures were above 21 °C (weekly average maximum temperature) for more than four weeks (Weeks 3 to 8 in Figure 3.3) which according to Pierce (1987) once the temperatures are raised to above 21 °C after vernalization, flower formation will subsequently take place. As outlined above, the temperature started to drop in Week 6 which might have led to devernalization, thus giving allowance for the plants to grow fully to their normal capacity to form a head, with the result that no visual bolting was observed.

During harvesting (five months after transplanting), however, about seven percent of the plants showed signs of bolting as they had inflorescence primordia in the axils of terminal leaves of the heads (with elongated cores (Figure 3.8 and Figure 3.9). The effects of the low temperatures the plants were exposed to during the early stage of growth could have been the cause. Daly & Tomkins (1995) reported that when the cabbage plants are exposed to temperatures of 13 °C or less for two or more weeks, they will be vernalized. After low temperatures during the winter period, the temperatures increased at an increasing rate thus prompting the plants to form inflorescence primordia. This is seen as a critical point for the formation of flowers. After the low temperature exposure, there should be an immediate increase in temperatures for plants to shoot to flowering. The last three weeks as of the experiment (Figure 3.3) shows that the temperature had an instant increase which could have played a major role in initiating bolting in the cabbage plants. Thus, the plants could have experienced two low temperature treatments one in the growth chambers and a further one in the open field. Therefore, the sudden change from low (cold) temperatures to warmer temperatures during the production cycle may potentially initiate bolting in cabbage plants. On another note, avoiding warmer temperature in spring may play a major role in minimising cabbage bolting to susceptible cultivars.

Figure 3.8 shows the head and the core lengths of the two cultivars in different treatments that had inflorescence primordia (A1 to A8) and those without (B1 to B6) inflorescence primordia. Statistical analysis was not possible due to the inadequate number of heads that produced inflorescence (eight heads had inflorescence out of 120 plants). The linear trend line (red) shows that the core lengths for the plants which did not show inflorescence were shorter than those with inflorescence. The core length presents an important factor/cue in determining cabbage bolting. The trend lines also show that the gap or difference between the core length and the length of the cross sectional area was less for the plants which had inflorescences while it was more on the plants without inflorescences. The difference between the core length and length of the cross sectional area (after genetic consideration) may be another important factor that can be taken into consideration when identifying bolted cabbage plants.

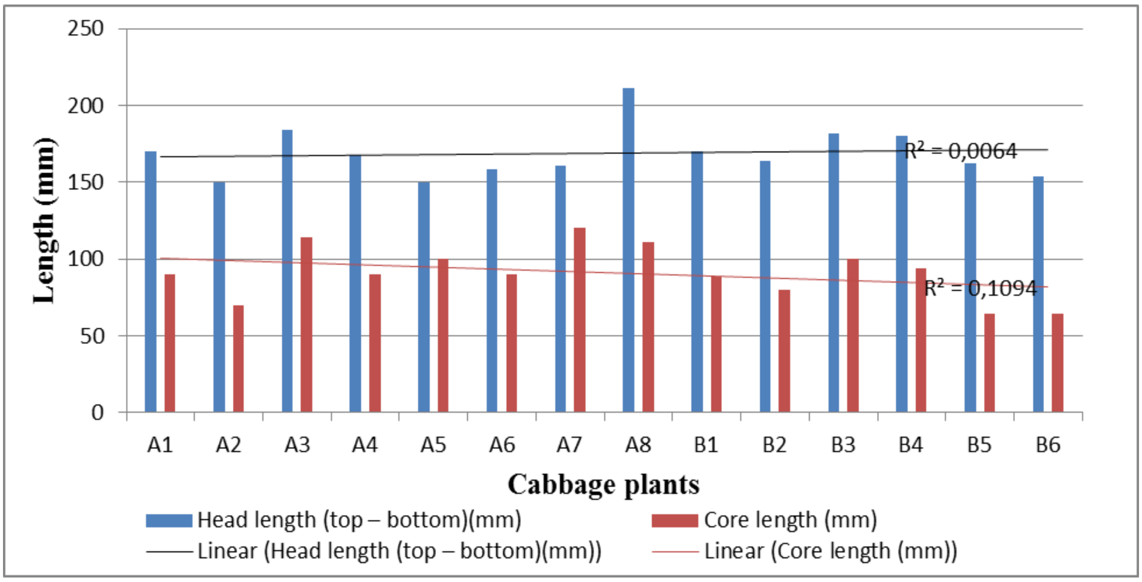


FIG 3.8: Core length and head length of 'Conquistador' and 'Grandslam' cabbage heads with inflorescence (A1 to A8) and without inflorescence (B1 to B6). 'Grandslam' 5 °C (A1, A2, A3, A4 and B1), 'Grandslam' 10 °C (A5 and B2), 'Grandslam' 15 °C (B3), 'Conquistador' 5 °C (A6 and B4), 'Conquistador' 10 °C (A7 and B5) and 'Conquistador' 15 °C (A6 and B8)

'Grandslam' is more sensitive to bolting and 'Conquistador' is a cultivar less sensitive to bolting. Therefore, 'Grandslam' could have "easily sensed" the changes in temperatures and responded by bolting. This was confirmed by the examination of longitudinal sections (Figure 3.10).

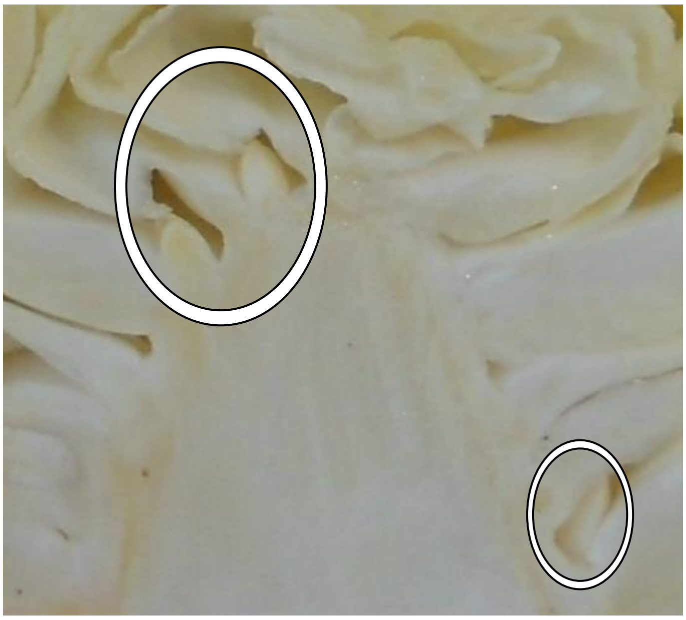


FIG. 3.9: A cut-surface section of a 10 °C treated 'Grandslam' cabbage head. Within the circles are inflorescence buds developing on leaf axils

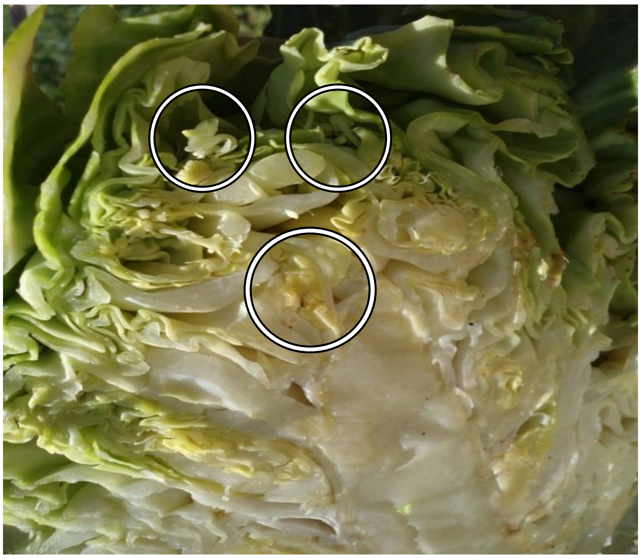


FIG. 3.10: A 5 °C treated 'Grandslam' cabbage cultivar with developing inflorescence (inside circles)

3.3.2 Experiment 2: Effect of temperature on cabbage cultivars

As in Experiment 1, the plants exposed to 15 °C had a slower growth rate than plants exposed to 20 °C. The cultivars, as also presented in the first experiment, resembled almost the same growth pattern in relation to the temperature they were exposed to. Figure 3.11 (A) shows an example of a 'Grandslam' plant which was exposed to 10 °C and (B) shows a 'Grandslam' plant exposed to 15 °C night temperature for two months. Figure 3.11 (C) and (D) show the different cultivars in a growth chamber, immediately after the temperatures were increased to 20 °C night temperatures and 30 °C day temperatures.

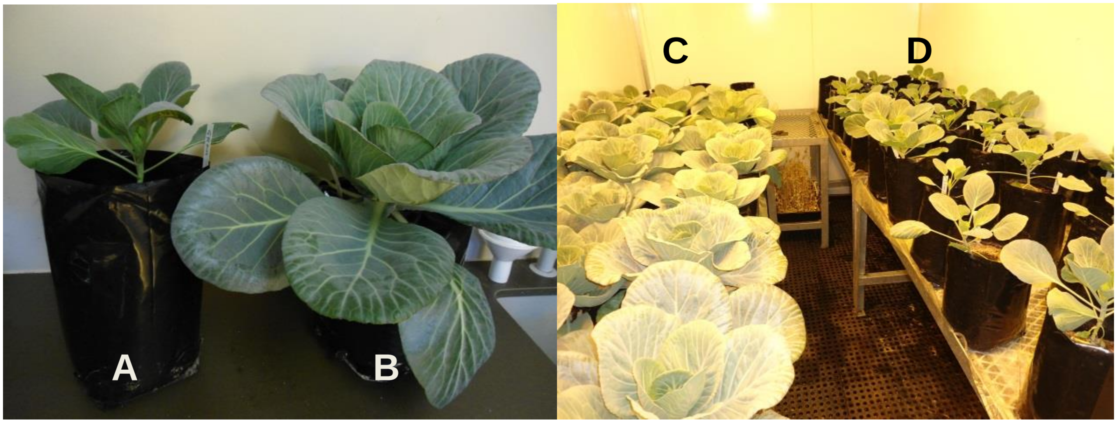


FIG 3.11: Cabbage plants after two months exposure to low temperatures. A – 'Grandslam' cabbage plant grown under 15 °C night temperature and B – 'Grandslam' cabbage plant grown under 20 °C. C and D show the two cabbage cultivars in a growth chamber (28 – 30 °C), immediately after the two months exposure to 20 °C and 15 °C temperatures respectively

Suppressed growth induced by low temperature had an effect on subsequent growth of the plants. This was seen by the non-heading of cabbages even after being exposed to high temperatures. Some plants remained in the cupping stage (Figure 3.12 D, E, F) with more non-heading leaves. This agrees with the over-wintered cabbages which did not form heads at Lanseria, South Africa, as observed during a farm visit. Park *et al.* (2013) confirmed that cabbage head development depends on a significant genotype-environment interaction. Head formation can be delayed directly due to low temperatures causing physiological and morphological alterations at both, cellular and tissue level (Seymour *et al.*, 2004). Park *et al.* (2013) also confirmed that the exposure of plants to above-optimal or below-optimal growth temperatures affects the enzymatic activities needed for many essential metabolic processes, including photosynthesis, carbon fixation and development.

Figure 3.12 shows the three cabbage cultivars with differences in head structure after exposure to high temperatures (30 °C). The plants from 15 °C night temperature treatments (A, B and C), had firm, compact and matured heads but they were very small in size. Cabbage plants from the 10 °C treatment did not form any heads as shown by D, C and F. Table 3.5 shows the small head mass obtained in this experiment. On average, cabbage head weight ranges above 4kg whereas the average maximum weight obtained in this experiment was 1.13 kg for 'Grandslam'. The eight grams weight by the 'Conquistador' exposed to 15 °C was as a result of no head formed in the plants as shown by Figure 3.12 E. Due to the sizes of the heads of this experiment and the non-development of bolting, no statistical analysis were conducted due to the small number of plants that had to be used in the small growth cabinets.

TABLE 3.5: Average cabbage head mass of three cultivars

Treatment (°C)	Mass with cover leaves (g)	Mass without cover leaves (g)
‘Tenacity’ 10	995	496
‘Tenacity’ 15	622	255
‘Conquistador’ 10	865	374
‘Conquistador’ 15	391	8
‘Grandslam’ 10	1133	588
‘Grandslam’ 15	517	177

FIG. 3.12: Cabbage plants pre-exposed to 10 °C (D, E and F) & 15 °C (A, B and C) and subsequently to high (30 °C) temperatures. A & D – ‘Grandslam’ plants, B & E – ‘Tenacity’ plants and C & F – ‘Conquistador’ plants

The headed ‘Grandslam’ cultivar had cracked heads (Fig 3.13), from the initial stage of cracking (A) to a stage at which the plant had a pointed head (C&D). The cracks were a sign of core elongation within the head (Figure 3.14). Only four plants showed core elongation in the whole experiment (30 evaluated heads). Two of these elongated cores were found in ‘Tenacity’ plants exposed to 15 °C and the other two were ‘Grandslam’ plants exposed to 10 °C. The core elongated rapidly which subsequently forced the head to crack as a result of leaves giving way to the elongating core. When a cabbage plant has been vernalized, the elongation of the core is associated with the formation of inflorescence buds both in the terminal bud and along the core in the leaf axils. Both, ‘Tenacity’ and ‘Grandslam’, are classified as highly-susceptible to bolting cultivars, but did not bolt, even when allowed to grow further. This phenomenon is probably an indication that two separate processes are involved in bolting, namely core elongation and inflorescence bud formation.

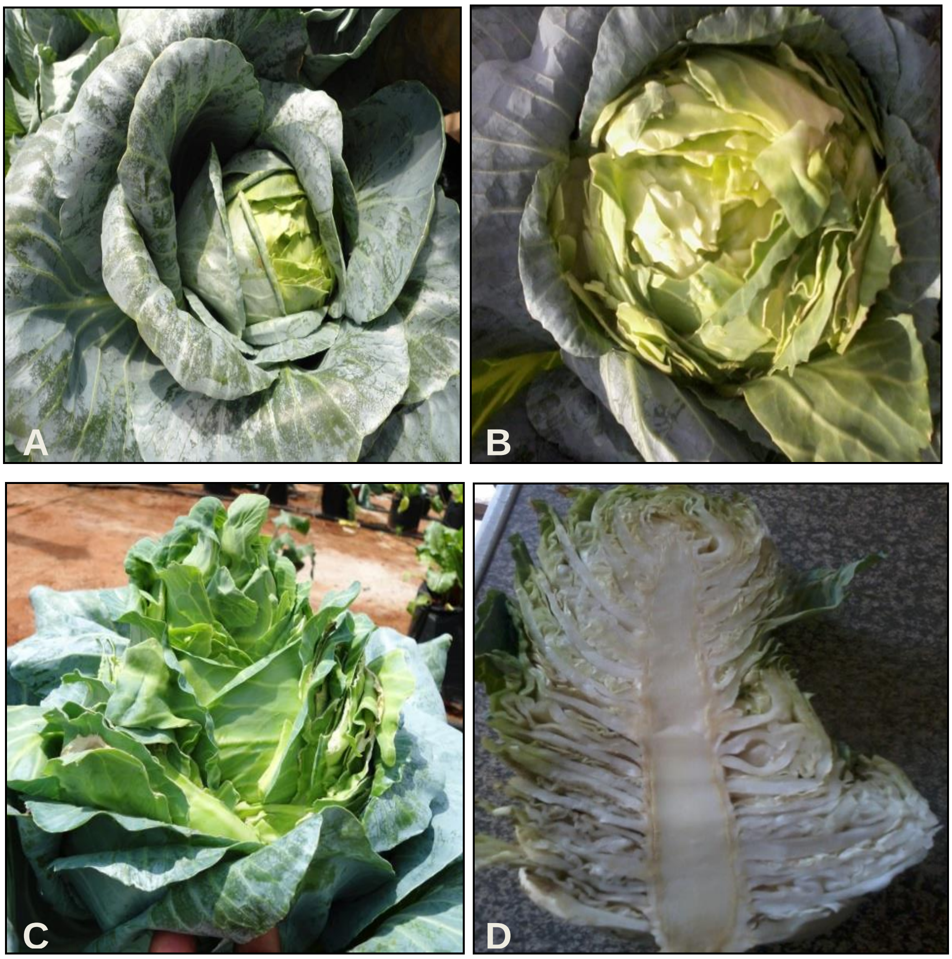


FIG. 3.13: A – A cracking ‘Grandslam’ (10 °C) cabbage plant, B – more and severe leaf tearing, C – elongated core with non-folding leaves and D – cross-section showing an elongated core of plant C

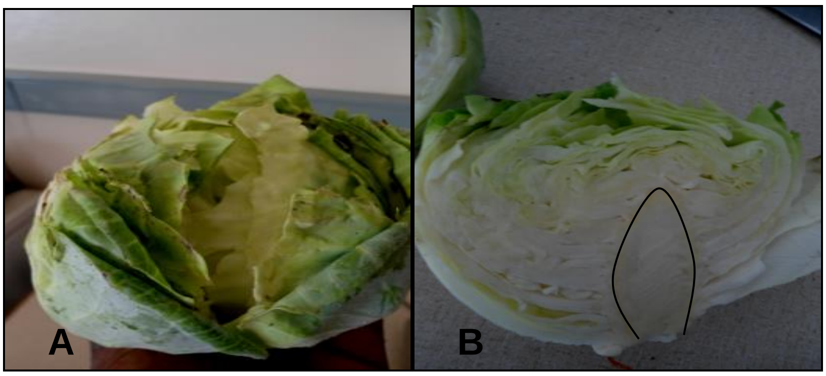


FIG. 3.14: Cracked ‘Tenacity’ (15 °C) cabbage head (A) full cabbage (B) longitudinal-section cut

3.4 Conclusion

The two experiments presented in this chapter show that exposure of 'Conquistador', 'Grandslam' and 'Tenacity' cabbage plants to low temperature regimes in the early stages of growth, before transplanting, affects the growth rate of such plants in subsequent growth stages. Cabbage head cracking maybe caused by temperature changes. Exposing plants to low temperatures may not be a limiting factor in producing good quality cabbage heads if plants are not exposed to higher temperatures immediately after being exposed to low temperatures.

The temperatures in the field for the first experiment (cupping growth stage) were less than 10 °C for about 10 weeks which may have acted as a second cold treatment to the plants. These may be an important factor, as most authors mention that temperatures less than 10 °C are good enough to vernalize cabbage plants in the cupping stage. The exposure to 10 °C temperatures could be a major factor in plant growth rate as some plants in the second experiment (seedling growth stage) did not form heads. The low winter temperature regimes the plants were exposed to in the field after treatment in the first experiment could have contributed to the unclear findings on the effect of low temperature on cabbage bolting.

CHAPTER 4

EFFECT OF LOW TEMPERATURE TREATMENTS OF TWO CABBAGE CULTIVARS AT EARLY AND LATE HEADING STAGES

4.1 Introduction

Previous experiments (Chapter 3 and 4) showed that seedlings and plants in the early cupping stage did not show visible signs of bolting after low temperature treatments. A more detailed experiment was carried out to determine the effect of low temperature treatments during early head development and fully headed cabbage plants on bolting. This necessity was prompted since after an over-wintering period, cabbage plants may bolt depending on the temperatures that were experienced during the over-wintering period. An open field experiment was also conducted to confirm some of the findings of Experiment 2 (Chapter 3). Therefore, the aim of this experiment was to determine the effect of low temperature treatments on early and late heading stages of cabbage.

4.2 Materials and Methods

4.2.1. Experiment 1: Response of cabbage plants in the early heading and fully headed stage to low temperature

The experiment was conducted in growth cabinets at the Experimental Farm of the University of Pretoria (25° 45 N, 28° 16 E, 1372 m above sea level). Cabbage plants at two different developmental stages, as outlined in Table 4.1, were exposed to low temperatures to induce bolting and subsequently exposed to high temperatures to allow inflorescence development. 'Conquistador', a cultivar less sensitive to bolting and 'Matador', a cultivar not prone to bolting were used for this experiment.

The period (ranging from 3 to 9 weeks) of low temperature exposure for the plants and the period (8 weeks) of exposure to high temperature are indicated in Table 4.1. An incubator fitted with fluorescent lights, controlled temperature and controlled photoperiod, was used for growing the two cabbage cultivars under the low temperatures. The cabinet had adequate light supply for the plants since according to Vandre (2011), maximum plant growth can be achieved through the use of white and cool fluorescent lights. The photoperiod in the cabinet was set at 11 hours day and 13 hours night to resemble Pretoria winter condition. A walk-in growth chamber that was used for exposing the plants to high temperatures following the low temperature treatment was set at a temperature regime of 30 °C for 12 hours during the day and 20 °C for 12 hours during the night.

Six-week-old seedlings were transplanted from seed trays to 10 cm diameter plastic pots and kept in these pots throughout the duration of the low temperature exposure. Prior to being exposed to high temperatures, the plants were re-transplanted into 10 litre black planting bags. Sand and coir mix was used on both pots and bags as the growing medium.

TABLE 4.1: Outline of temperature treatments on three cabbage development stage

Plant growth stage	**Period of low temperature exposure**	**Low temperatures**		**High temperature for 8 weeks**	
		7 °C Night temperature (13 hours)	**15 °C Day temperature (11 hours)**	**20 °C Night temperature (12 hours)**	**30 °C Day temperature (12 hours)**
Seedling	3, 5, 7, 9 weeks	X	X	X	X
Early heading	8 weeks	X	X	X	X
Fully headed	8 weeks	X	X	X	X

In the growth chamber (high temperatures), all cabbage plants in the different treatments were grown for a period of eight weeks, which should be sufficient to allow the plants to develop inflorescences, if induction occurred during the exposure to the low temperatures (Daly & Tomkins, 1995). Other than the development of inflorescence, the development of flower buds, head cracking, core elongation and change of leaf orientation within the head are some of the signs of bolting that were specifically observed throughout the experiment.

After eight weeks of exposure to high temperatures, plants were harvested; heads were weighed and cut lengthwise through the middle to determine core length and total length of the head and to look for signs of inflorescence development. The length of the cores in each treatment was compared with the length of the head, measured from the bottom to the top. Core terminal buds were also observed for signs of further inflorescence development.

4.2.2 Experiment 2: Over-wintering effects on cabbage growth and development

An open field experiment was also conducted concurrently with Experiment 1. Seedlings of both cultivars (‘Conquistador’ and ‘Matador’) were transplanted into field on the 3rd of May 2013 (Week 1 in Figure 4.3). The seedlings used were of the same age (six weeks old) as the seedlings used for Experiment 1. Eight plots (3 m by 5 m) were used for this experiment and each plot had 30 plants. The cultivars were allocated to the plots using the randomised complete block design and each cultivar was replicated four times.

For this experiment, fertilizer application and all other agronomic practices were the same in all the plots. Fertilizer 2:3:4 (38%) (600 kg/ha) was broadcast and ploughed into the soil before transplanting. Limestone ammonium nitrate [LAN (28 %)] (300 kg/ha) was applied as top-dressing fertilizer, five weeks after transplanting. Sprinkler irrigation was done twice a week, depending on the weather condition to provide about 25 mm of water per week. Throughout the entire growing period, there was no need for pest or disease management.

The plants were harvested in the first week of October 2013, which was five months after transplanting. Observations and measurements made were the same as for the previous experiment.

4.3 Results and Discussion

4.3.1 Experiment 1: Response of cabbage plants in the early heading and fully headed stages of to low temperature treatments

Plants exposed to 7 °C night and 15 °C day temperature for eight weeks showed a slow growth rate. They remained almost the same size (plant height and number of leaves) after being exposed to 20 – 30 °C for eight weeks as they were when removed from the low temperature treatment. The effect of the low temperature was so severe that plants could not grow further after subsequently being introduced to high temperatures. The plants produced non-folding leaves (non-heading) (Figure 4.1). Therefore, there was no head formation on plants exposed to 7 °C night and 15 °C day treatments during the seedling stage and no bolting occurred, in accordance with previous experiments (Chapters 3 and 4).

FIG. 4.1: 'Grandslam' cabbage exposed to 7 °C for 8 weeks followed by 8 weeks at 20 – 30 °C

The low temperatures had an effect on growth and development of plants (Table 4.2 and Table 4.3). The weight of cabbage heads after harvest showed that the plants were very small with an average weight of 597 g for early heading, 507.5 g for fully headed 'Conquistador' heads and 690 g for early heading and 1135.5 g for fully headed 'Matador' heads. Both cultivars have an average standard head weight of 3 -5 kg.

In this experiment, however, cabbage heads of 'Conquistador' exposed to low temperatures during early heading and headed stages of growth showed signs of bolting. Cores (stems) of the bolting cabbage heads were much longer than the non-bolting heads. It was observed that the cores of the bolted heads grew up to near the apex of the head (Table 4.3). Both growth stages (early and fully headed) of 'Matador' did not show any signs of bolting and had small heads with thick cores which showed that they were not induced to flowering.

TABLE 4.2: Head mass, core length and head length for 'Conquistador' and 'Matador' pre-treated 8 weeks exposure to 7 °C night and 15 °C day temperatures (early heading)

Cultivar	HMCL (g)	HMOCL (g)	LL (mm)	CL (mm)
'Conquistador'	570	245	90	75
	445	140	84	70
'Matador'	1165	600	85	40
	1110	610	80	40

Key: HMCL – Head mass in grams with cover leaves
HMOCL – Head mass without cover leaves
LL – Length of head in mm
CL – Core length in mm

TABLE 4.3: Head mass, head length and core length for 'Conquistador' and 'Matador' after of 8 weeks exposure to 7 °C night and 15 °C day temperatures (fully headed)

Cultivar	HMCL	HMOCL	LL	CL
'Conquistador'	495	220	70	40
	700	355	80	45
'Matador'	775	345	75	47
	605	330	65	37

Key: HMCL – Head mass in grams with cover leaves
HMOCL – Head mass without cover leaves
LL – Length of head in mm
CL – Core length in mm

All 'Conquistador' plants exposed to cold during early head development developed inflorescences (Figure 4.2A), while the fully headed plants had only inflorescence buds (Figure 4.2B) in all the heads. All the 'Conquistador' cabbage heads that were exposed during the early heading phase had long cores and loose heads. There were open spaces (gaps) between leaf axils along the stem with inflorescence buds in the leaf axils which made the heads to be 'loose heads'. Terminal buds and buds in leaf axils in close proximity to the terminal buds contained partly developed inflorescences. The arrows in Figure 4.2A show developing inflorescence buds, after plants had partly developed inflorescences (circle in Figure 4.2 B).

In fully headed plants exposed to low temperatures, the head remained firm and compact, while the inflorescence buds were growing within them. The presence of inflorescence buds was a sign of initial stage of bolting inside the head. There was no head cracking observed in this experiment.

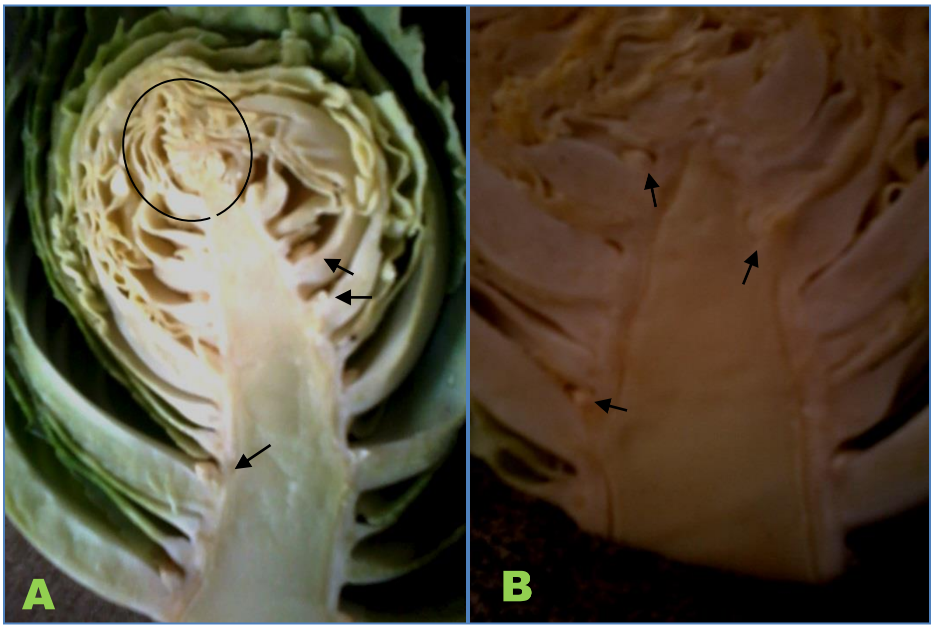


FIG. 4.2: Longitudinal sections of 'Conquistador' cabbage heads showing early stages of bolting: A – Axillary inflorescence buds (arrows) and inflorescence developing from apical bud (circle) at the early heading stage. B – Apical part of head showing axillary inflorescence (arrows) at the fully headed stage

4.3.2 Experiment 2: Over-wintering effects on cabbage growth and development

The temperature data presented in Figure 4.3 was taken from a weather station of the University of Pretoria situated about 100 m away from the plot. Average minimum temperatures were low between end of May and August 2013 (weeks 5 - 15) were low. The average minimum temperatures were below 10 °C temperature conducive to vernalizing 'Conquistador' plants. Guttormsen (1981) stated that one week of growth at an average temperature of 12 °C is sufficient to initiate the flowering process. The average monthly maximum temperatures for May, June, July and August were 20.65, 19.38, 19.33 and 19.01 °C, respectively. The period between May to August had optimum maximum temperatures for growth as Adeniji *et al*. (2010) reported that the temperature at 18-20 °C are optimal. The minimum temperatures in the last two weeks of August (Weeks 15 and 16) began to increase which may have been necessary for elongation of the cabbage core (seed-stalk).

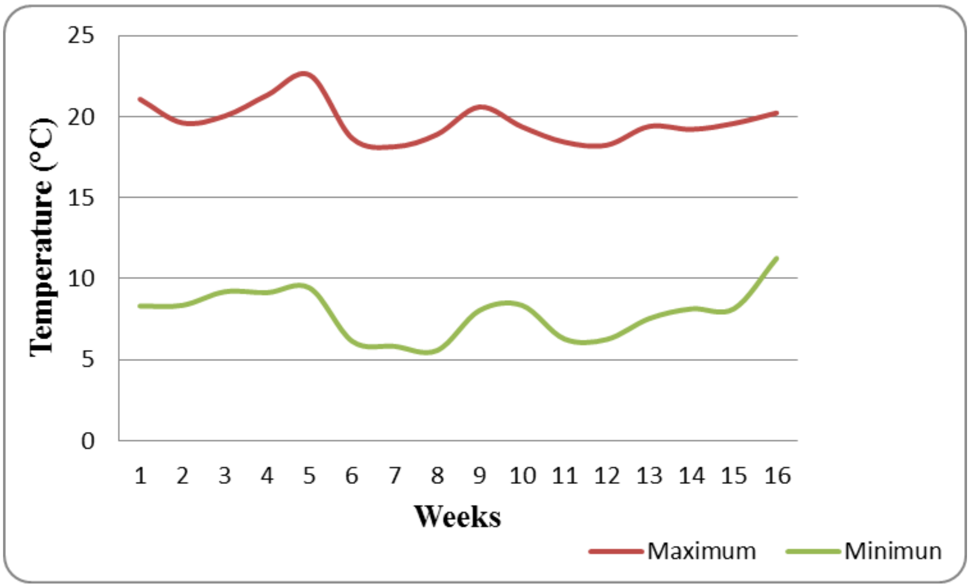


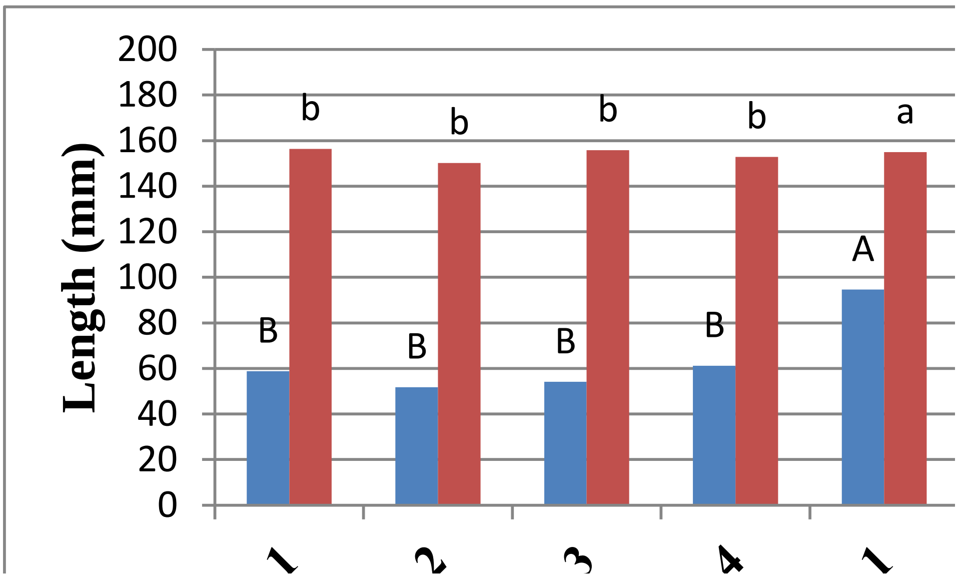
FIG. 4.3: Average weekly minimum and maximum temperatures recorded at the experimental site for the period May (1-5), June (5 -8), July (9-12) and August (13-16) 2013

The cold temperatures, to which cabbage plants were exposed (Figure 4.3) had an effect on plant growth. This was revealed by the long period of growth from transplanting to harvesting (4 months). Generally, plants are normally harvested after about three months from transplanting. This long period of growth allowed the plants to be exposed to low temperatures during their development. The exposure of the plants to low temperatures from transplanting to cupping stages delayed head development, but could not vernalize the plants. The compactness of the cabbage head after harvesting as presented in Figure 4.5 (A, B and C) showed that vernalization may not have taken place on the plants prior to head formation in all the plants. Leaf axils along the vegetative stem are close to each other and the leaves were compact within the heads.

There was no significant difference ($P \geq 0.05$) in mass of cabbage heads with wrapper leaves between the two cultivars (Figure 4.4). Therefore, the effect of winter (low temperature) on the cabbage growth for both cultivars was the same. However, there was a significant difference ($P \leq 0.05$) between the two cultivars regarding cabbage heads without cover leaves which may mean that the difference within the heads without cover leaves was as a result of genetic differences.

When the longitudinal sections of the cabbage heads were examined, 20% of the ‘Conquistador’ heads were found to possess elongated cores (Figure 4.4 and 4.5 B), while the 'Matador' heads possessed un-elongated cores. The 'Conquistador' inflorescence development in the apical bud and the axillary buds (shoots) showed along the core of the leaf axils. The core elongation and inflorescence development showed that vernalization had taken place on the plants at some point during their growth. Statistically, a significant difference ($P \leq 0.05$) between the two cultivars was found, with the cultivar 'Conquistador' having longer cores and head height than 'Matador'.

In normal 'Matador' cabbage heads there was a greater difference between the cabbage head length and the core length (Figure 4.4). In the case of 'Conquistador' cabbage heads, the difference between the head length and core length was small, indicating the onset of bolting, as was indeed seen in the developing inflorescences (Figure 4.5).



Bars with the same letter are not significantly different at 5% level of confidence

FIG. 4.4: Core length and head height for over-wintered 'Matador' and 'Conquistador' cabbage cultivars

Inflorescence development on axillary buds and terminal buds was evident in cut cabbage head (Figure 4.5 F, G and H). Cabbage heads containing developing inflorescences were compact, firm and round, when observed from the outside; there were no external signs of bolting.

The elongated core made space available for the axillary buds to develop after the plants were vernalized (Figure 4.5 B, C and D). The axillary buds with young inflorescences had a yellowish colour (Figure 4.5 D and E) since buds were absent in non-vernalized heads (Figure 4.5 A).

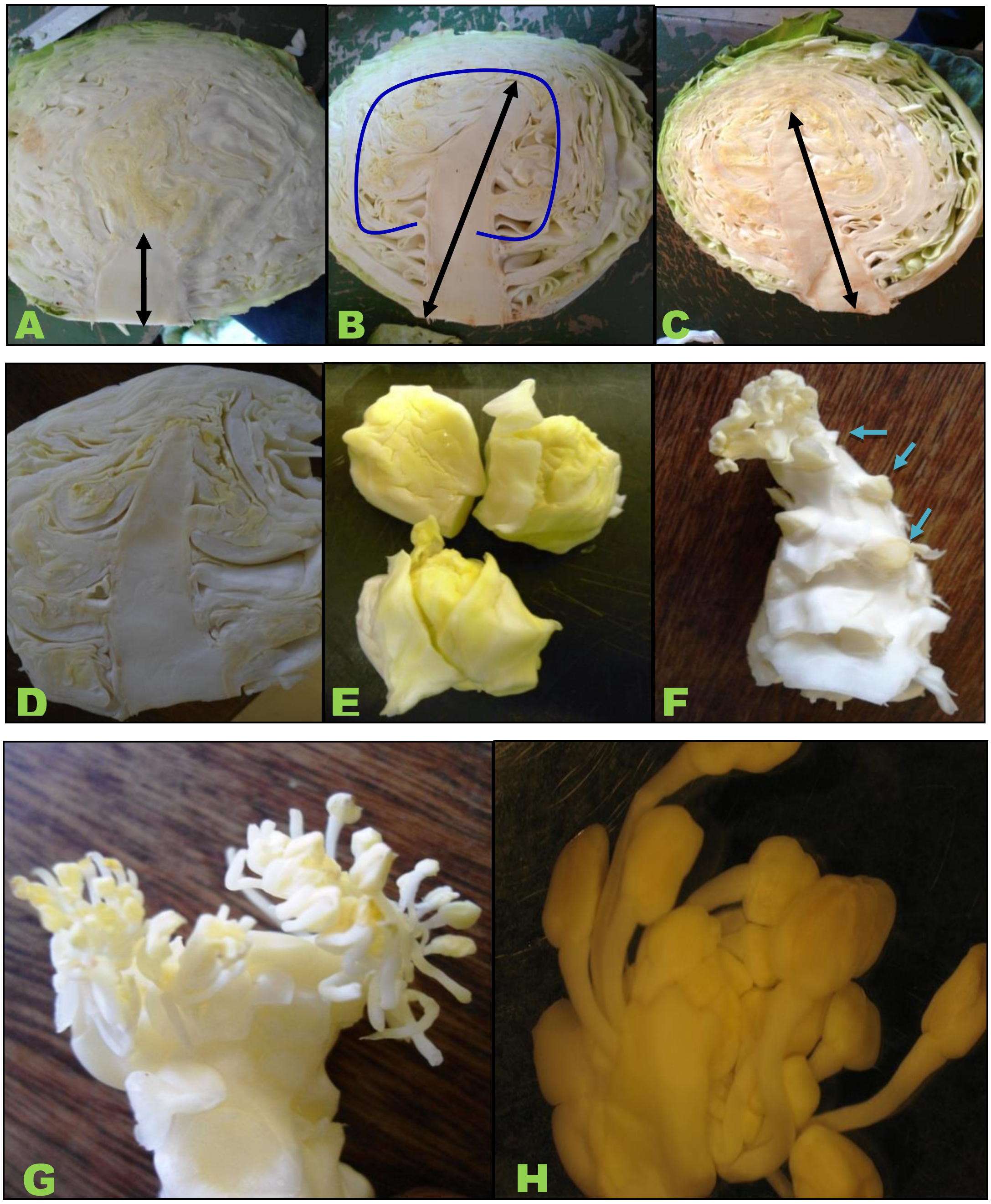


FIG. 4.5: Formation of compound inflorescence in cabbage head. A – 'Matador' cabbage head with normal and compact head. B & C – 'Conquistador' cabbage head with elongated core and highlighted by arrows. D – bolting head of 'Conquistador' as removed from the highlighted by blue line in B with yellowish flowering side shoots. E – Side shoots removed from D which has developing inflorescences. F – Core with arrows shows vivid bud points and the terminal bud having developed inflorescence. G – Terminal bud with several flower buds and inflorescence. H – Flower buds on an inflorescence

4.4 Conclusions

Cabbage cultivars that are susceptible to bolting, like 'Conquistador', do not seem to bolt if exposed to low temperatures during the early growth stages, such as the seedling and early cupping stages; however they do seem to bolt if exposed to the low temperatures during the early and full heading stages of growth.

CHAPTER 5

GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

Bolting is a problem that affects susceptible cabbage cultivars exposed to low winter temperatures when left in the field until the onset of warm spring temperatures. In this dissertation, cabbage cultivars were exposed to different temperature regimes during the seedling, cupping, early heading and fully headed growth stages.

The 7 °C night and (Experiment 1, Chapter 4) supplied evidence that a combination of 7 °C night and 15 °C day temperature impair plant growth in all cabbage growth stages. Experiment 1 (Chapter 3) showed that seedlings exposed to low temperatures may experience growth stress that may be 'released' by transplanting the seedlings to more favourable temperature regimes. Kalisz and Cebula (2006) had also reported that exposing seedling plants to low temperature prior to transplanting is one of the techniques used to acclimate plant so that an increased tolerance to bolting during adverse winter conditions; which however, Experiment 2 (Chapter 3) and Experiment 1 (Chapter 4) showed that an extended exposure of plants of all growth stages to low temperature regimes may lead to irreversible growth effects, such as non-folding leaves, non-head formation and stunted growth of the plants. Exposing seedlings and transplants in the cupping stage to 7 °C and 10 °C night temperature regimes for three or more weeks may lead to non-head formation.

All experiments conducted showed that the hybrid cabbage cultivars used were not induced to bolting by low temperature regimes during the seedling and cupping stages. This is contrary to the popular belief that cabbage bolting could be induced or triggered during seedling production or immediately after transplanting. This contradicts findings by Guttormsen (1981) who reported that many small seedling plants at transplanting will bolt if exposed to continuous, low vernalizing temperatures.

In this dissertation, a combination of 7 °C night and 15 °C day temperatures at the early-heading and fully-headed growth stages clearly induced bolting in cabbage. This result was supported by findings on over-wintered cabbage plants which, after heading, were exposed to less than 10 °C in the open field during the winter period. These cabbage plants ('Conquistador') formed inflorescences within the heads, a clear sign of bolting. The occurrence of bolting as induced by these temperature regimes was in line with findings by

Silver *et al.* (1982), Pierce (1987), Lin *et al.* (2005) and Kumar *et al.* (2009) who stated that 4 °C to 10 °C temperature regimes are necessary to induce bolting in cabbage plants. Maxia *et al.* (2004) also stated that 4 °C to 10 °C are also necessary for inducing Chinese cabbage plants to bolt. Findings in this dissertation pertaining triggering of bolting during the early heading and fully headed stages of growth during exposure to low temperature and over-wintering makes an important contribution to the production of cabbages..

Cabbage plants with advanced inflorescences or inflorescence buds within a matured cabbage head may continue to bolt before or after harvesting which is a serious challenge to farmers. These findings supported reports by Shoemaker (1947) who stated that cabbage varieties with compact heads are likely to bolt, posing a serious threat on the quality and profitability of cabbage heads. These findings clearly indicate that bolting heads may lead to a considerable decrease in the quality of the heads.

In this dissertation, evidence is supplied that certain cabbage cultivars can be induced to bolt by exposing them to 7 °C night temperature and 15 °C day temperature regime in the early heading and fully headed stages; however, seedlings of the same cultivars could not be induced to bolt.

Inadequate facilities have limited the scope of the research, as replication of treatments in growth chambers was a challenge. Reliable and adequate facilities for the duration of experiments are recommended. The use of only hybrid cabbage cultivars for this research may not be the best option since similar open pollinated cultivars may be more prone to bolting and may give differing results from hybrid cultivars. More research on the actual micro-climatic conditions which cabbage plants are exposed to on the different affected areas can be valuable to farmers. More attention should be placed on the stage of cabbage growth and duration of low temperature exposure to gain a more detailed understanding of cabbage bolting.

General Summary

Cabbage hybrid cultivars were exposed to a combination of different temperature regimes in growth chambers and over-wintered in an open field to determine at what growth stage bolting is triggered.

Exposure of cabbages to low temperatures (10 °C) during the seedling and/or cupping growth stage had no significant impact on hybrid cultivars. The plants can avoid the effects of temperature with regards to bolting, even though growth can be severely impaired by such low temperatures. Low temperatures were found to have an adverse effect on leaf size and leaf internode length; however, low temperatures do not seem to have a significant effect on leaf number during the seedling stage. Low temperature had an effect on stem length, distribution of leaves along the stem and within the cabbage head, shape of the leaves during heading phase, including head formation and head size.

Cabbages exposed to low temperatures (7 °C) in growth chambers and cabbage over-wintered in the field demonstrated that cabbages in the early-heading and fully-headed growth stages are highly susceptible to bolting; particularly in certain hybrid cultivars. Exposure and over-wintering at cabbages to an average minimum temperature of less than 10 °C in growth chambers or in the field induced bolting in susceptible plants. This emphasizes that in susceptible hybrid cultivars, cabbage heading is a critical growth stage in which bolting can be induced. Early signs of bolting in early heading stage include an elongated core, inflorescence buds on leaf axils along the core and less folding leaves within the head.

The findings in this dissertation confirm that over-wintered cabbage plants in areas which experience a considerable transition from low winter temperature regimes to high spring temperature regimes are highly susceptible to bolting. The adhering to sowing guidelines from production companies is therefore critical for sustainable cabbage production in South Africa.

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APPENDICES

APPENDIX A: AVERAGE TEMPERATURES FOR GREYTOWN, PRETORIA AND BLOEMFONTEIN FOR 2010, 2011 AND 2012 FROM 1ST OF APRIL TO THE 31ST OF OCTOBER

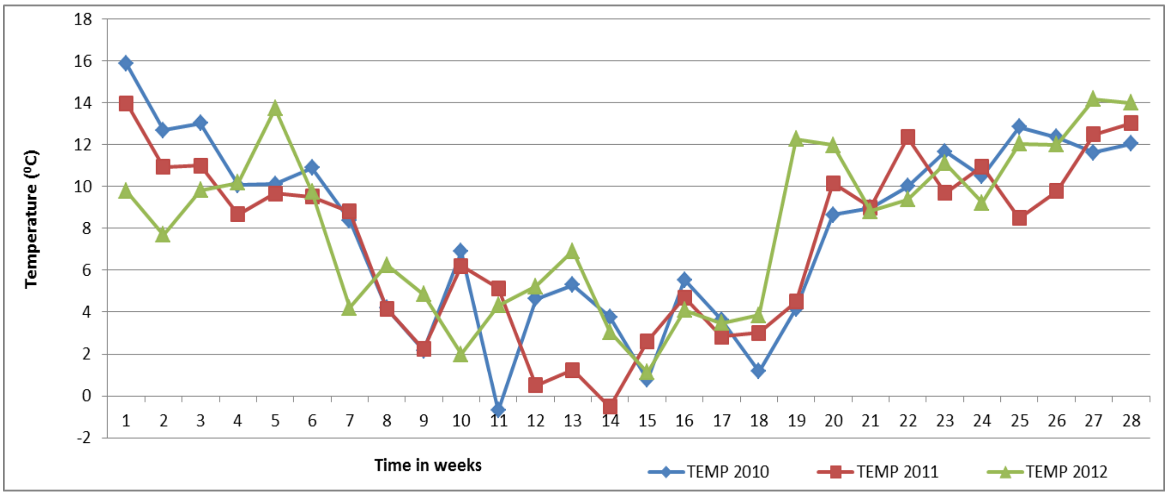

FIG. A-1: 2010, 2011 and 2012 average weekly minimum temperatures for Greytown area

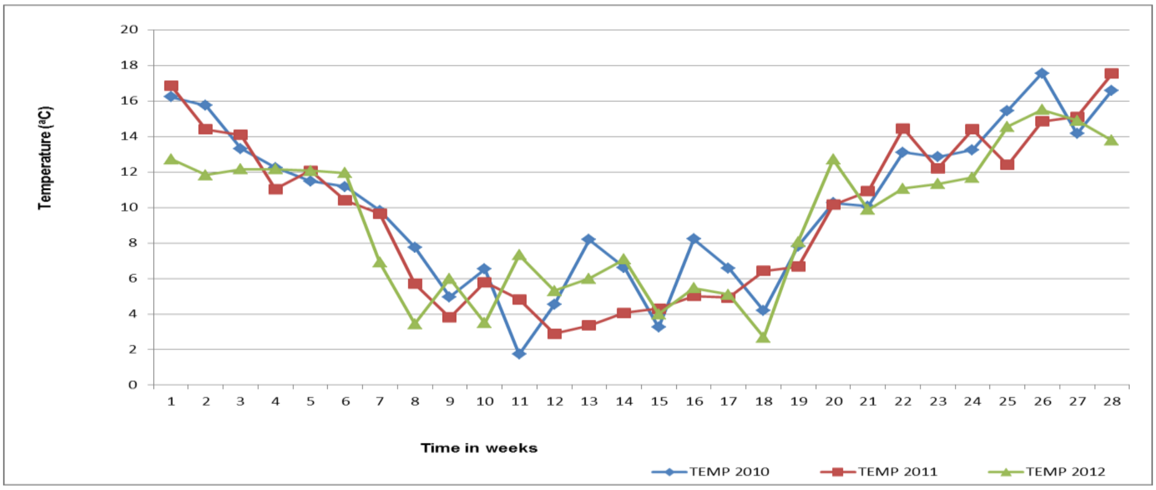

FIG. A-2: 2010, 2011 and 2012 average weekly minimum temperatures for Pretoria

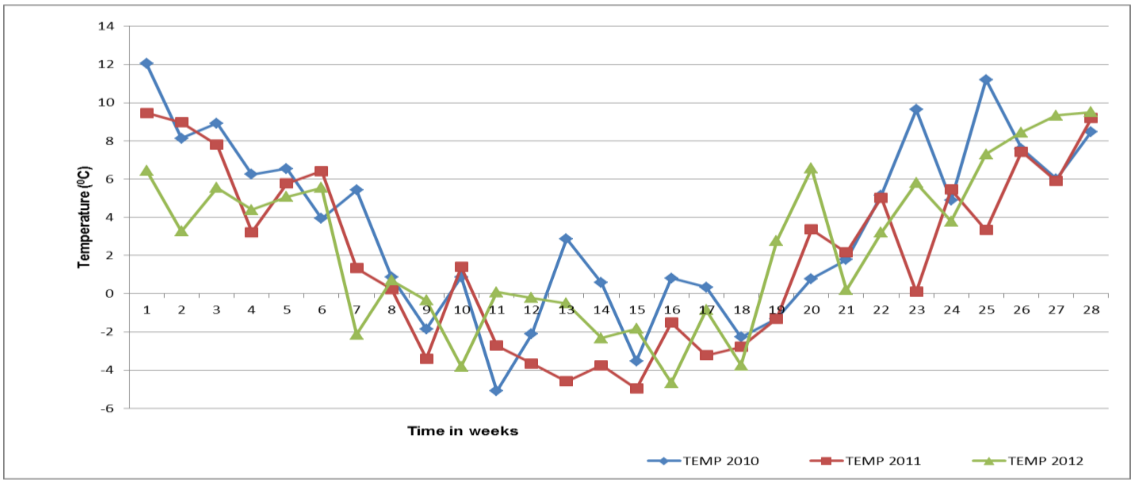

FIG. A-3: 2010, 2011 and 2012 average weekly minimum temperatures for Bloemfontein

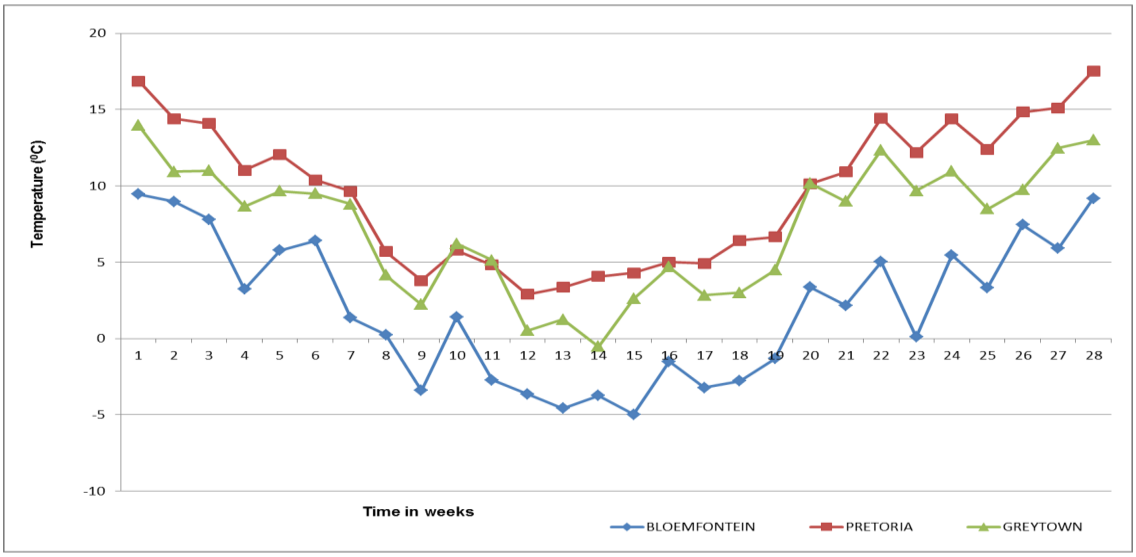

FIG. A-4: 2011 average weekly minimum temperatures for Greytown, Pretoria and Bloemfontein areas

APPENDIX B: EFFECT OF TEMPERATURE ON SEEDLING PRODUCTION

FIG. B-1: Cabbage side shoots. (A) = side shoots formed with no main cabbage head. (B) = one side shoot formed alongside the main cabbage head. (C) = side shoots formed under the cover leaves of the main cabbage head

APPENDIX C: EFFECT OF LOW TEMPERATURE ON CABBAGE TRANSPLANTS

Table C-1: Head-length and core length of bolted cabbage plants treated with 4 °C and 10 °C temperature regimes

Treatment	Head length (top – bottom)(mm)	Core length (mm)	No. of bolted heads	Total number (%) of bolted heads
Grandslam 4 °C	17	9	1	40
Grandslam 4 °C	15	7	1	
Grandslam 4 °C	184	114	1	
Grandslam 4 °C	168	9	1	
Grandslam 10 °C	15	10	1	10
Conquistador 4 °C	158	9	1	10
Conquistador 10 °C	161	12	1	10
Conquistador 15 °C	211	111	1	10