GRAIN SORGHUM IN THE HYBRID-ERA, 1957-2008:
YIELD WITH HYBRID ADVANCMENT AND IMPROVED AGRONOMIC PRACTICES

by

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AN ABSTRACT OF A DISSERTATION

Submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

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ABSTRACT

Grain sorghum yield has notably increased from the beginning of hybrid production and commercialization in the late 1950s. The yield increases were the result of improved agronomic practices and hybrid advancement. The objectives of my research were: (1) to determine the magnitude of yield change in the hybrid era in irrigated and rainfed sorghum production, (2) to determine the contribution of agronomic and hybrid changes for yield in the hybrid era, (3) to investigate changes in sorghum morphology, physiology, and water use that contributed to yield increases, (4) to investigate changes that accompanied yield increase with hybrid improvement, and (5) to understand sorghum water and nutrient use and variations between hybrids in these regards. Fifty-two years of grain sorghum hybrid performance trial data (1957-2008), were analyzed and greenhouse and field studies were conducted on five selected hybrids to meet our objectives. The greenhouse and field studies were conducted from the summer of 2007 to the fall of 2009 on five selected hybrids, each representing a decade from the past fifty years. Results indicated that there was an increase in hybrid yield of nearly 50 kg ha^{-1} yr^{-1} in dryland sites over the 52 yrs (1957-2008) analyzed. Irrigated grain sorghum yields, however, remained unchanged over the same period. Agronomic practices such as planting date, phosphorus fertilizer use, and planting density changed over these years but were not found to contribute to increased dryland sorghum yields. There was no difference found between old and new hybrids tolerance to different densities. Hybrid advancement and increased nitrogen fertilizer application were responsible for changes in dryland yields. Total water use changed with hybrid advancement. New hybrids used the greatest total water and also had greater root-to-total biomass ratio than the old hybrids. Leaf biomass was also greater for the newest hybrid. There was a difference in amount of total nutrients extracted by hybrids, and there were differences among hybrids in allocation of nutrients to different tissues. In general the yield focus of sorghum hybrid development was effective in dryland sorghum production, likely because of intentional or inadvertent selection of hybrids with better drought tolerance. Results indicated that breeding programs created hybrids with improved morphological characteristics that might have resulted in better resource use (water and nutrient) and ultimately increased yield.

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I dedicated this work to three most important people in my world:

My Mother, Mulu Kebede

For investing in my education more than anything else and envisioning me at this position.

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For participating in this project (from threshing sorghum, and entering data, to evaluating my power point presentations), and for taking care of me and our baby when I was busy working.

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For coming to my world, and for her smiles and claps which make my life the happiest ever.

Chapter I

GENERAL INTRODUCTION & BACKGROUND OF THE STUDY

Grain sorghum belongs to the Poaceae (grass) family, genus *Sorghum,* and it is scientifically called *Sorghum bicolor* ssp *bicolor*. Sorghum was consumed as early as 8000 BC (Smith and Frederiksen, 2000). Domestication of sorghum began around 4000-3000 BC in Ethiopia and surrounding countries (Dillons et al., 2007). From there, it was distributed along trade and shipping routes to other parts of Africa, through the middle East to India, and along the Silk Route to China (Dicko et al., 2005).

Domestication from wild species and introduction to different environments have changed sorghum over time. For example, early domestication of sorghum led to large, non-shattering and compact panicles through increased number of rachis/branches within the panicle, decreased distance between kernels, increased seed size, and an overall increase in yield from the original sorghum landraces (House, 1985).

After sorghum was domesticated and became more important as a staple crop, the major focus shifted to adaptation. For that purpose, photoperiod-sensitive and tall varieties were converted to photoperiod insensitive and short hybrids, so as to adapt to the environment and management systems in temperate and subtropical environments. After adaptation, issues of disease, drought, and improved yield became significant. Therefore, selection of drought tolerant, pest and disease resistant, and high yielding hybrids continues to sustain and improve sorghum yields (Reddy et al., 2006).

One of the key tools used in sorghum improvement is hybrid production. Although heterosis in sorghum was demonstrated as early as in 1927 (Conner and Karper, 1927), hybrid sorghum production and commercialization began in the United States (Doggett, 1988) within two years from the discovery of cytoplasmic male sterility by Stephens and Holland (1954). It is assumed that sorghum production in the world is 19% higher than it could have been without the use of hybrids (Duvick, 1999).

GRAIN SORGUM IN THE UNITED STATES AND YIELD ADVANCES SINCE THE 1950's

The first deliberate grain sorghum varieties introduced to the United States were Brown Durra and White Durra in 1874 from Egypt. In 1876, two Kafir varieties, Whitehull White and the Red, were introduced from South Africa. Milo was introduced between 1880 and 1885. Shallu was imported from India in 1890. Introduction of the Kaloliang group sorghums was made between 1898 and 1910 from China. In 1905 another Kafir variety called Pink was introduced from Africa. Feterita and Dwarf Hegari were introduced in 1906 and 1908, respectively, from Sudan (Swanson and Laude, 1934; Murty, 1999).

Today, the United States is the highest producer and world's major exporter of sorghum (FAO, 2005). Nearly 50% of the annual grain sorghum production is exported from the United States and around 12% is used for ethanol production. The average value of the crop is estimated to be more than a billion dollars per year (USDA, 2009).

From 1874 to 1955, sorghum yields were approximately 1.2 to 1.4 Mg ha^{-1} (Murty, 1999). The USDA reports yields as low as 0.7 Mg ha^{-1} in the early 1900's (Fig. 1.1). At present, hybrid adoption is nearly 100% and average dryland yields can exceed 5 Mg ha^{-1}. From an analysis of 61 yrs (1930-1990) of sorghum yield data, Eghball and Power (1995) reported a 50 kg ha^{-1} yr^{-1} yield increase in the United States. Based on studies conducted at USDA-ARS Conservation and Production Research Laboratory in Bushland, Texas, Unger and Baumhardt (1999) reported that sorghum grain yield increased by 139% (1.6 to 3.8 Mg ha^{-1}) from 1956 to 1997.

The yield gain over the past 50 years was not exclusively due to genetic improvement. There have been substantial changes in agronomic practices, such as agricultural mechanization, weed and pest control, tillage, and fertilizer use. For instance, the number of work animals in the United States declined from 21.6 million in 1900 to 3 million in 1960 and they were almost completely replaced by tractors in 1970 (Dimitri, 2005). In addition, from 1960 to 2007, the consumption of N, P, and K fertilizer in the United States increased by 4.5, 1.7, and 2.3 fold, respectively (USDA-ERS, 2009). Timmons (1970) reported a number of herbicides introduced and commercialized in the 1950's and 1960's. Appleby (2005) reviewed a history of weed control since 1970 and indicated the introduction of new herbicides and an increasing attention of integrated methods for controlling weeds with non-chemical as well as chemical methods in the United States and Canada.

Thirty-five to 40% of the total yield gain in grain sorghum is assumed to be due to hybrid advancement. Improvements in cultural practices, like nitrogen fertilizer, irrigation, and tillage, are assumed to contribute 60 to 65% of the yield gain (Duvick, 1999). Unger and Baumhardt (1999) indicated that 93% of the 139% yield increase they reported was a result of increased soil water at planting due to changes in management practices; the other 46% was attributed to improved hybrids.

RESEARCH GAPS

An increase in grain sorghum yield response from hybrid introduction to recent years and factors, which contributed to these yield increases, were reported by few authors as indicated in the previous section. However, these reports fail to show independent comparison for irrigated and dryland production. The knowledge of yield responses in irrigated and dryland sorghum production would have helped evaluate the capacity of our breeding programs by answering the question, "Was the yield increase in sorghum due to changes in genetic yield potential or increased tolerance to biotic and abiotic yield-limiting factors?". Studies that compared old and new corn hybrids reported little change in corn yield potential under irrigated conditions, but dryland corn yields have increased because of improved drought tolerance (Duvick and Cassman, 1999).

Secondly, most existing reports include yield data from the early 1950s. Use of sorghum hybrids was not common before the end of the 1950s, and analyses that include these data inflate the yield gain due to improvement in hybrids. To our knowledge, none of the studies on sorghum showed the yield response due to hybrid advancement alone, i.e., within the hybrid era. Sorghum hybrids were first made available to farmers in 1957, but accounted for 90% of the planted area by 1960 (Smith and Frederiksen, 2000). Therefore, it is crucial to evaluate yield within the hybrid era.

Thirdly, the contribution of agronomic factors and hybrid improvements reported for sorghum were not exhaustive. In the last fifty years, many agronomic changes (planting date, planting density, nutrient management) and environmental changes such as changes in precipitation, temperature, and increased in atmospheric CO_2 might have occurred and contributed to yield increase. However, none of the studies exhaustively reported the contribution of each of these factors.

Fourthly, none of the studies which indicated yield increase due to hybrid improvement clearly justified what changed within hybrids and brought about the increase in yield. Several studies have compared old and new corn hybrids to determine what factors contributed to a yield increase over time (Tollenaar, 1991; Duvick, 2005). Yet, few studies have tried to relate hybrid improvement of sorghum with changes in crop yield. Mason et al. (2008) found that yield increases in corn resulted from an increase in one yield component (ear m^{-2}), but yield increases in sorghum were not related to yield components. However, that study reported only yield components (panicles m^{-2}, kernels $panicle^{-1}$, and kernel weight) and did not report other morpho-physiological or phenological characters that might have contributed to yield increase. Genetic improvements are often associated with and manifested in the plants' phenology, physiology, and morphology. Therefore, it is important to investigate how genetic changes (hybrid improvement) gave rise to yield increases in terms of changes in morphology, physiology, and resource use.

In addition, changes that accompanied yield increase with hybrid improvement are seldom reported for sorghum. The changes could be in seed quality, nutrient uptake pattern, and nutrient allocation, which might be unrelated to yield but occur in conjunction with an effort to increase yield. The knowledge of these changes also helps to understand the positive and negative consequences of our breeding efforts.

OBJECTIVES AND HYPOTHESIS

To fill the research gaps cited above, the present study was initiated with the following general objectives:

(1) To determine the magnitude of yield increase in irrigated and rainfed sorghum production in Kansas due to hybrid improvement and changes in agronomic practices

(2) To determine what aspect of grain sorghum, i.e., morphology, physiology, and water use, has changed with hybrid improvement and contributed to this yield increase and also to determine what accompanied this yield increase.

On the basis of prior findings for corn and the knowledge that sorghum hybrid selections were made primarily for dryland environments, we hypothesized that improved drought tolerance is the factor that contributed most to sorghum yield changes with hybrid advancement. Our hypothesis for the second objective was that change in sorghum yield due to hybrid advancement should be explained by morphological, physiological reasons, by resource use, or by improvement in allocation of nutrients among hybrids.

We expected a consistent change in one or more character with the advancement of hybrids

A GENERAL APPROACH TO THE STUDY

In order to test the first hypothesis and meet the first objective, we investigated yield trends of sorghum in different Kansas counties from yield performance trial reports (Chapter 2). Multi-location grain sorghum performance trials have been conducted in Kansas since 1957. The main objective of the performance trials is to help growers choose hybrids by providing unbiased information on the relative grain production potential of many hybrids available in the state (Kansas State University, 1957-2008). Each year, from 1957-2008, a minimum of 48 hybrids (in 1957) to a maximum of 195 hybrids (in 1992) from 10-38 entrants (companies and institutes) has been tested in different counties of Kansas (Fig. 1.2).

In 1957, the performance trial was conducted in six locations. In 2008, the performance trials were conducted in 19 locations. We used performance trial data from two and four counties for the irrigated and dryland yield analysis, respectively. These sites were selected because performance trials have been conducted at each of these locations from approximately 1957 to 2008. Based on the data available in the grain performance trial reports and data from meteorological stations in or around the trial sites, we further analyzed factors that contributed to the yield improvements.

As a second step, we selected five hybrids, one from each decade from the beginning of hybrid deployment to the present (Table 1.1). These hybrids were selected based on the following criteria: 1) they represent release periods of 1954-1964, 1964-1974, 1974-1984, 1984-1994, and 1994-2005; 2) they yielded average and above average during those release periods; (3) they are of similar maturity, and (4) seed was available for study.

Two greenhouse studies and one field study were conducted on the selected hybrids. The first greenhouse study focused on investigating the contribution of changes on water use, morphology, and physiology towards yield change of hybrids (Chapter 4). The second greenhouse study focused on investigating the changes in nutrient use and nutrient allocation within hybrid advancement (Chapter 6). The field study investigated the response of hybrids to plant density (Chapter 7).

This report, therefore, includes the results of the analysis of the performance tests, the greenhouse and field experiments, and reviews on water use (Chapter 3) and nutrient use (Chapter 5) of grain sorghum.

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Table 1.1 Hybrids used in greenhouse and field studies, their year of release and other selected characteristics

Hybrid	Year release	Maturity†	Flowering DAE††	Plant Height cm	Head Type†††
RS610	1956	Medium late			compact
P848	1962	Medium late	70-73	111-137	Semi open
P833	1970	Medium late	74-78	121-137	Compact
P8585	1976	Medium	69-72	96-127	Medium
P8358	1987	Medium late	68-75		Semi open
P85G46	2005	Medium late	65-70	121-132	Semi compact

† Sorghum hybrids can be grouped into three big maturity groups: Early (100-110 days to mature), medium (111-120 days to mature), and late (121-131 days to mature). Hybrids can fit into these groups or in between.

††DAE -Days after emergence

†††Sorghum head, panicle, can also be grouped into two big groups: Loose (open), and Compact. Hybrids can fit into these groups or fit in between.

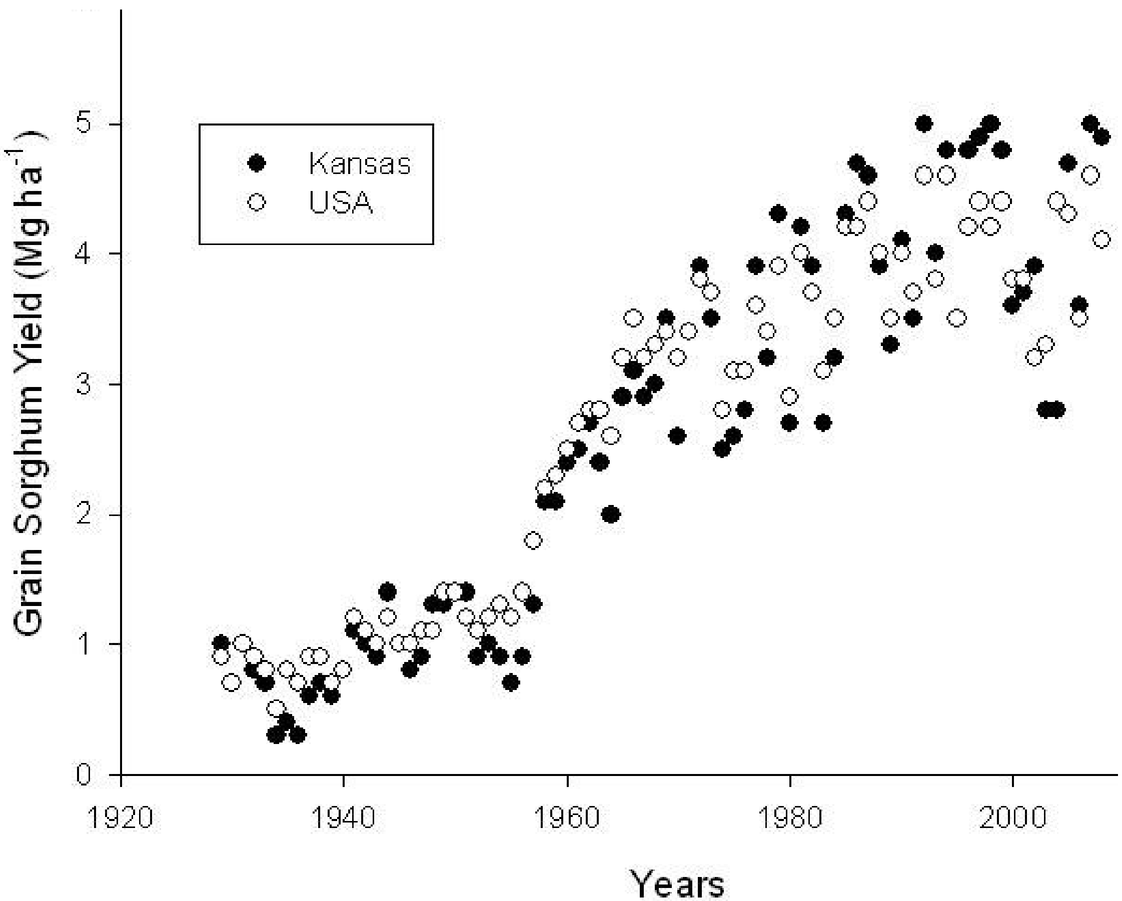

Figure 1.1 The average yield of grain sorghum in the United States from 1924-2009. Data from (USDA-NASS).

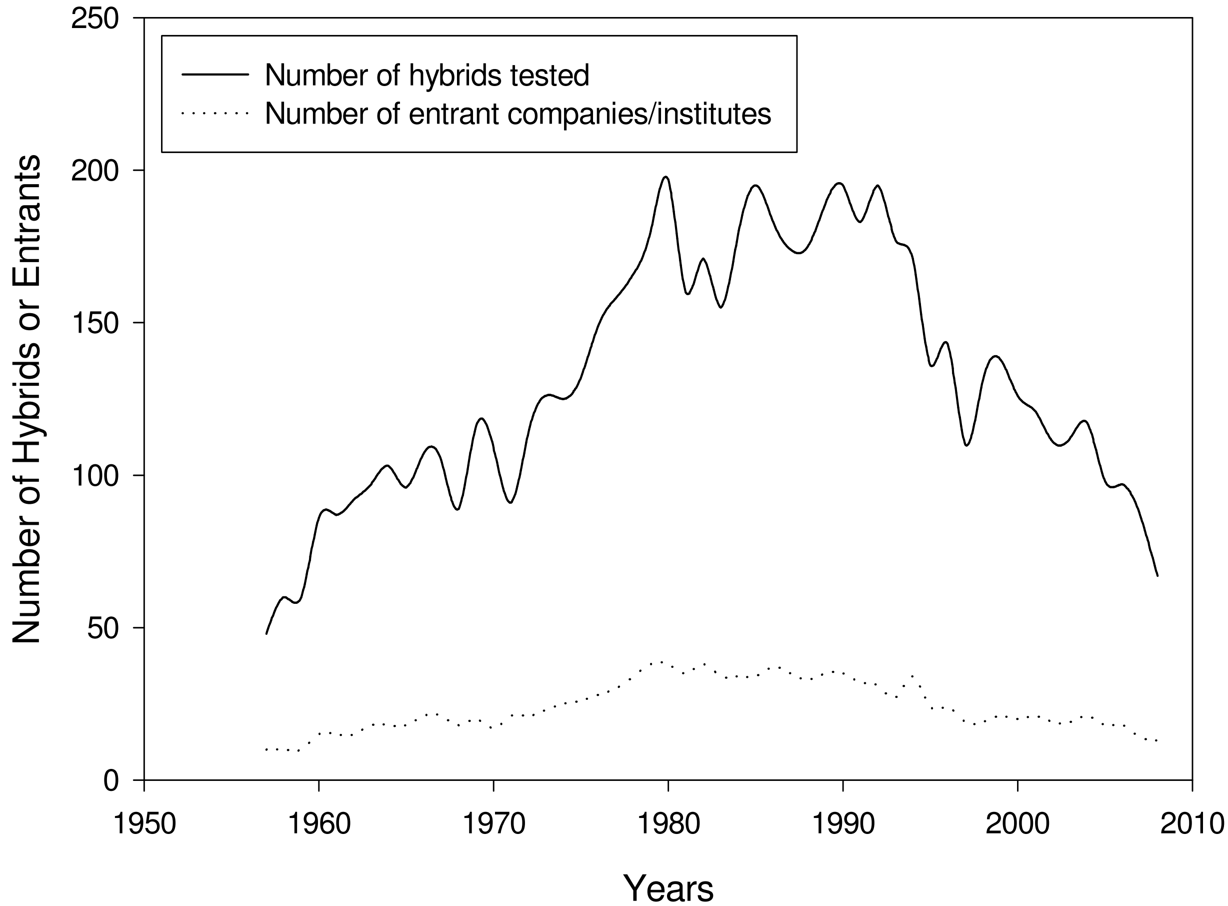

Figure 1.2 Number of hybrids tested and entrant companies and institutes that participated in Kansas grain sorghum performance trials from 1957 through 2008.

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Chapter II

Grain Sorghum Yield with Hybrid Advancement and Changes in Agronomic Practices from 1957 through 2008

ABSTRACT

Sorghum grain yield has improved since the deployment of hybrid sorghum in the mid-1950s. However, information on the contribution of different factors to this yield increase for irrigated and dryland sorghum production is scarce. The objective of the present study was to determine the magnitude of change in irrigated and dryland sorghum yields with hybrid improvement and changes in agronomic practices. Data from selected irrigated and dryland grain sorghum performance trials conducted in Kansas, USA from 1957 to 2008 were analyzed. The mean yield of the highest-yielding hybrid over years was 9.3 Mg ha^{-1} at irrigated sites and 5.8 Mg ha^{-1} at the dryland sites. There was an increase in hybrid yield of nearly 50 kg ha^{-1} yr^{-1} in dryland sites over the 52 yrs analyzed. Irrigated grain sorghum yields, however, remained unchanged over the same period. Agronomic practices such as planting date, phosphorus fertilizer use, and planting density changed over these years but were not found to contribute to increased dryland sorghum yields. Hybrid advancement and increased nitrogen fertilizer application were responsible for changes in dryland yields. The yield focus of sorghum hybrid development was effective in dryland sorghum production, likely because of intentional or inadvertent selection of hybrids with better drought tolerance.

Grain Sorghum Yield with Hybrid Advancement and Changes in Agronomic Practices from 1957 through 2008

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Chapter III

GRAIN SORGHUM WATER REQUIRMENT: A REVIEW

ABSTRACT

Sorghum yields are maximized at optimum environmental conditions. However, sorghum is a drought tolerant crop and often preferred by many producers in cases of expected water stress. The objectives of the present review was to understand the water requirement, the effect of water stress, existence of hybrid variation in drought tolerance, and to compile possible solutions that would help narrow the potential yield and actual yields in dryland sorghum. Reports of more than seventy peer reviewed journals, extension publications, books, and web pages were reviewed. Results suggest that due to its root system, the ability to maintain stomatal opening at low levels of leaf water potential, high osmotic adjustment, waxy bloom substance on leaves and stem, and due to adjustment in leaf angle and rolling in low water conditions grain sorghum tolerates and resists drought better than many other cereal crops. However, drought responses of sorghum do not come without a yield loss. Water stress at the vegetative stage alone can reduce yield more than 36% and stress at reproductive stage can reduce yield more than 55%. Our review found that 80% of sorghum in the world is under dryland production. We deduced that by focusing on improved drought tolerance, we can double current dryland sorghum yields without need of improving genetic potential. Results also suggested existence of genotypic variation for drought tolerance among sorghum hybrids due to possible physiological differences or vice versa. Based on our review, possible management options to reduce the effects of water stress in drylands and possible areas of research are suggested.

A number of factors limit sorghum yields. Of these, drought or prolonged dry periods; delayed rainfall; nutrient deficiencies; weeds, insects, and diseases; cool, wet weather at planting or harvest; lodging; excessive or erratic rainfall; early frost; snow and extreme cold conditions; washing rain and hail; high temperature; hot, dry summer; high-windy conditions, and bird attacks could be cited (Assefa and Staggenborg, 2010).

In analyzing 52 yrs of sorghum production in Kansas, we found out that drought was mentioned as a major yield limiting factor for about 30 of the 52 yrs (Assefa and Staggenborg, 2010; Table 3.1). It was not only the most frequently mentioned, but it was also one of the most described in different forms, i.e., late summer drought, mid summer drought, August drought, drought in early and late August, drought and high temperature, drought and early freeze, heat and drought, extensive drought or prolonged dry period, delayed rainfall, and below normal rainfall. These expressions shows complexity of drought in terms of intensity, timing, length, and its conjunction with other factors like freeze and heat (extreme temperatures).

In addition to its complexity and frequency, drought in sorghum production can be the core cause for other major production problems. For example, drought can reduce nutrient uptake by roots and induce nutrient deficiency by decreasing diffusion rate of nutrients from soil to root, creating restricted transpiration rates, and result in impaired active transport and membrane permeability (Alam, 1999; Viets, 1972). Many sorghum pests and diseases are also aggravated by drought due to weak growth and a weak defense system, i.e., stalk rot diseases (charcoal rot and Fusarium stalk rot) (Edmunds, 1964; Seetharama et al., 1987; Zummo, 1980); sorghum ergot (Bandiopadhyay et al., 1996); sorghum downy mildew; and sooty strip.

Grain sorghum is tolerant to drought and often grows in environments where water stress is expected. A study showed that grain sorghum had a yield and economic advantage in dryland regions over corn due to its better drought and temperature tolerance (Staggenborg et al., 2008). It was also reported that grain sorghum is capable of taking up more nutrients from soil under drought conditions than corn (Lamaire et al., 1996). However, data also show that sorghum performance under dryland is far less than irrigated sorghum yields (Assefa and Staggenborg, 2010). From these we can deduce that drought tolerance has a cost related to it.

The objectives of the present review were to understand the water requirements of sorghum, the yield loss in dryland sorghum production due to drought, hybrid differences in drought tolerance, and to suggest possible solutions that would help narrow the potential yield and actual yield in drylands production. In order to attain these objectives, reports of more than seventy papers from peer reviewed journals, extension papers, and web pages were reviewed.

LITERATURE REVIEW

GRAIN SORGHUM WATER REQUIRMENT

Sorghum water use is mainly affected by its growth stages and environmental demands. Hybrid differences also exist in water use (Kidambi et al., 1990), due to differences in growth habit and maturity. For high production, a medium to late maturing sorghum cultivar (maturity within 110 to 130 days) requires approximately 450 – 650 mm of water during a growing season (FAO, 2002; Tolk and Howell, 2001). However, the daily requirement varies greatly depending on the growth stage.

Early in the growing season, the average daily water use is low. Approximately 1 to 2.5 mm day^{-1} could be enough to avoid water stress. This period is roughly the first 25 -30 days (up to approximately the seventh leaf stage). The water requirement then increases to around 7 to 10 mm day^{-1} until the boot stage. Maximum daily water use occurs from the boot stage until after anthesis. Daily water requirement decreases gradually during grain fill as leaves begin to senesce and the crop matures (Krieg, 1983; McWilliams, 2002, Stichler and Fipps, 2003).

About 90% of the total water used by sorghum is extracted from 0 to 1.65 m soil depth (Rachidi et al., 1993). The rooting depth of sorghum, however, can extend to about 2.50 m (Stone et al., 2002). The water depletion zone for sorghum will vary with growing stage. Water stored at deeper soil depths (below 1.0 m) are an important source of stored water at the end of the growing season (Moroke et al., 2005).

FACTORS THAT CAN AFFECT SORGHUM WATER USE & WATER USE EFFCIENCY

Environmental conditions like rainfall, temperature, relative humidity, solar radiation, and wind can affect water use of sorghum. Crop water use is a function of the crop factor and existing weather conditions. Under mild climatic conditions, water use of sorghum is lower than in climates with high evapotranspiration demand (Tolk and Howell, 2003). A mild climatic condition constitutes moderate temperature (20 to 25 °C), low wind speed and solar radiation, and a humid environment. Even though sorghum is a

C_4 plant, elevated atmospheric CO_2 has also been reported to reduce its water requirements (Conley et al., 2001).

Soils vary in water and nutrient holding characteristics and resistance to root penetration. A study showed that sorghum performed well in well irrigated clay soils (Tolk et al., 1997). In places where irrigation or precipitation is not sufficient, loam soil is preferred for grain sorghum production because of its high plant available water holding capacity. In soils having high bulk density, root growth might be restricted and water use will be negatively affected.

Soil management practices affect evapotranspiration by altering the heat balance at the soil surface and by changing the water exchange rate between the soil and the atmosphere (Hatfield et al., 2001). Reduced tillage systems, for example, decrease the incoming heat energy, which is capable of evaporating water, and change the exchange rate between soil and atmosphere and trap vaporized water. Grain yield response to water supply was found greater with no tillage than conventional tillage (Stone and Schlegel, 2006). In addition, Unger and Baumhardt (1999) showed that the major yield increase in sorghum production since the 1970's is mainly attributed to an increase in soil water content due to conservation tillage.

Diseases, insects, and weeds affect sorghum water use by affecting the plant's physiology and growth. Plant management practices, like application of required nutrients and application of appropriate disease, pest and weed control systems, will decrease the water requirement by increasing the use efficiency of the plant.

Planting date and planting density can also affect grain sorghum water use by altering canopy development (Baumhardt et al., 2007). Optimizing planting date and planting population, based on potential supply of water, minimizes opportunity for plant water stress that could be caused by high water demand (Krieg, 1983).

EFFECT OF WATER STRESS ON GRAIN SORGHUM YIELD

Sorghum can produce yields in semiarid regions where other grain crops often fail. However, grain sorghum yields are maximized when all environmental conditions are optimum. The highest recorded sorghum yield is 20 Mg ha^{-1} (Boyer, 1982). Many other studies in the United States reported above 8 Mg ha^{-1} yield for fully irrigated sorghum (Assefa and Staggenborg, 2010). The average yield for drylands, however, is about a half or less than reported irrigated yields.

As with all crops, sorghum grain yield is dependent on water supply (soil water at planting and in-season precipitation). A summary of 30 yr of data from Tribune, KS, indicated that every mm of water, above 100 mm, resulted in an additional 16.6 kg of grain yield (Stone and Schlegel, 2006). However, the relationship between grain yield and water is complex because yield is sensitive to water deficits at certain growth stages (Garrity et al., 1982a). Therefore, grain yield is highly dependent on distribution of rainfall or irrigation, according to demand of crop at each stage of growth, than on just total water available through the growing season. Howell and Hiler (1975) reported that yield response of grain sorghum was not strongly correlated to seasonal ET but was highly dependent on timing of the ET deficit.

Yield is sensitive to water stress and the effect of water stress on yield depends on: severity of the stress, duration of stress, growth stage of the crop at the time of stress, genotype, and the combination of all these factors (Garrity et al., 1984b; Salter and Goode, 1967; Younis et al., 2000).

Sorghum can tolerate short periods and non severe water deficit. However, long-term and severe stress can affect sorghum growth and the final yield. Eck and Music (1979) studied effect of various periods of water stress on irrigated grain sorghum at the early boot, heading, and early grain filling stages. Their report indicated that 13 to 15 days of stress did not affect grain yield. Twenty-seven to 28 days stress at early boot, heading, and early grain fill, however, reduced the yield by 27, 27, and 12%, respectively. Thirty-five and 42 days of stress beginning at boot stage, reduced yield by 43 and 54%, respectively. A study by Lewis et al. (1974) showed that a soil water potential drop to -13 bars from late vegetative to boot stage reduced grain sorghum yield by 17%. The same water potential drop from boot to bloom and milk through soft dough stages caused 34 and 10% reductions in yield, respectively. Inuyama et al (1976) reported 16 and 36% yield reduction due to 16 and 28 days of water deficit during the vegetative stage. In the same study, a 36% yield reduction was reported due to 12 days of water deficit during boot stage. Withholding 100 mm of irrigation water early 6-8 leaf stage and heading to bloom reduced sorghum grain yield by about 10 and 50 %, respectively (Jordan and Sweeten, 2007).

EFFECT OF WATER STRESS ON EMERGENCE, STAND ESTABLISHMENT, AND VEGETATIVE GROWTH

Among other factors moisture is important for seed germination (Arau et al., 2001). The embryo in the seed is dormant and highly tolerant to desiccation. After seed start to germinate and emerge, however, it would be susceptible to moisture stress (Blum, 1996). Water stress of seedlings could be caused by drought, high soil temperature, or high salt concentration during seeding and germination. Even if it is a rare occurrence under field condition, due to low amount of water requirement at early stage, water stress at the seeding stage can affect sorghum seed germination and emergence. Water stress at the seedling stage will reduce endosperm weight of the planted seed, growth of coleoptile, mesocotyl, radicle, shoot and root of sorghum (Sharma et al, 2004; Wondimun et al., 2005; Jafar et al., 2004). Sorghum stand establishment is dependent on seed germination and emergence. Drought can cause loss in a sorghum crop after full emergence before plant establishment (Blum, 1996).

Water stress reduces the rate of cell expansion and ultimately cell size and consequently, growth rate, stem elongation and leaf expansion (Hale and Orcutt 1987). Therefore, it decreases plant height and rate of leaf appearance. Sorghum leaf area is also reported to be reduced with water stress. Garrity et al. (1984) reported that a 14-26% reduction in photosynthesis by water stressed sorghum was accounted for a decrease in leaf area. Blum and Arkin (1984) also reported a significant leaf area reduction due to drought before a decrease in stomatal conductance.

In most cases sorghum root to shoot ratio has been reported to increase under water stress (Younis et al., 2000; Salih et al., 1999). The increased ratio is mainly due to a decrease in shoot growth rather than in an absolute increase in root growth under stress. However, there are reports of an absolute root weight increase under stress. This is due to diversion of significant amounts of assimilates to root growth which could be used to produce grain under non-stressed conditions (Wright et al., 1983).

EFFECT OF WATER STRESS ON REPRODUCTIVE GROWTH

Sorghum sensitivity to drought stress, like many grain crops, is greater during reproductive stages compared with the vegetative stage (Doorenbos and Kassam, 1979; Kramer 1983). Before the seventh leaf stage, average daily water use of sorghum is low and drought stress is less likely to occur in most production scenarios. As the water use of sorghum increases during boot to early grain filling stages, it is much easier to rapidly deplete stored soil moisture and suffer drought stress. Drought stress from boot stage through approximately ten days after anthesis will severely affect yield.

Water stress during reproductive stages can stop the development of pollen and ovules and prevent fertilization and/or induce premature abortion of fertilized ovules (Saini, 1997; McWilliams, 2002). Sorghum yield is a function of the number of harvested panicles, seeds per panicle, and individual seed weight. These most important components of yield are more dependent on duration and severity of drought during reproductive stages. Eck and Music (1979) reported that yield decreases due to water stress at early boot were due to both reduced seed size and seed number and yield reduction due to stress at heading (or later) was due to just reduced seed size.

EFFECT OF WATER STRESS ON PHYSIOLOGY AND BIOHEMICAL TRAITS

Severe water stress can cause closure of stomata. The closure of the stomata result in low stomatal conductance and low transpiration rates (Cechin, 1997; Salih et al., 1999). It is also reviewed that CO_2 assimilation by leaves is mainly reduced due to the closure of stomata in drought stress conditions (Farooq, 2009).

A reduction in photochemical efficiency of photosystem II (PSII), activities of phosphoenolpyruvate carboxylase (PEPcase) and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) were reported for severe water stress conditions (Vinita et al, 1998). In addition to the closure of stomata, a reduction in activity of PEPcase, a reduced RubisCO regeneration and functionality, and an inhibited functional activity of PSII, lowers the net photosynthetic rate (Shangguan et al.,1999).

An increase in the rate of photorespiration under severe drought condition can be deduced due to closure of stomata and an increase in the internal concentration of oxygen and a decrease in internal CO_2 concentration. An increase in reactive oxygen in cells result in injures to sorghum cells due to peroxidation (Farooq, 2009).

A reduction in leaf area and net photosynthesis and an increase in photorespiration rates eventually reduce total dry matter production in drought conditions (Perry et al., 1983; Terbea et al., 1995).

DROUGHT TOLERANCE AND AVOIDANCE MECHANISMS OF SORGHUM

The prolific root system, the ability to maintain stomatal opening at low levels of leaf water potential, and high osmotic adjustment are some of the mechanisms that help sorghum cope with drought (Johnson and Turner, 1978; Machado and Paulsen 2001; Turner, 1974;).

Many crops cannot extract water from deep soil profile and are unable to utilize apparent available water. Sorghum can extract water from deep in the soil profile and can remove most of the apparent available water (Cabelguenne and Debaeke, 1998). Sorghum can do this because it has many secondary roots per unit of primary roots compared with other cereal crops. For example compared with corn, sorghum has twice as many secondary roots per unit of primary roots (Martin, 1930).

Sorghum has the ability to maintain stomatal opening at low levels of water potential and under a wide range of leaf turgors. Turner (1974) reported that sorghum guard cells remained open over a wide range of leaf turgor (-11 bars to -1 bar) compared with corn and tobacco. The same result was reported earlier by Sanchez-Diaz and Kramer (1971). This adaptation of sorghum enabled the crop to maintain a higher rate of CO_2 exchange than other crops at high level of water stress.

Sorghum also has a high osmotic adjustment. It lowers its osmotic potential due to net solute accumulation in response to water stress. In the case of high soil water deficit, the osmotic potential in the leaves will decline and will minimize a significant water loss that could occur from leaf opening (Fekade and Daniel, 1991).

Increasing water stress can cause a decrease in the leaf potential of sorghum and at low leaf potential, around -14 bars, stomata will close, the abscisic acid level will become elevated, and the amount of starch in the bundle sheath chloroplasts will be reduced. If the leaf potential gets much lower than this, near – 37 bars, swelling of the outer chloroplast membrane occurs. Reorganization of the tonoplast also occurs to form small vacuoles from the large central vacuoles. This maintenance of tonoplast integrity is an important factor in the ability of sorghum to withstand drought unlike other crops like corn (Giles et al, 1976).

Under normal circumstances plants produce antioxidants to detoxify reactive oxygen that can cause lipid peroxidation (McKersie and Leshem, 1994). Water stress can cause lipid membrane peroxidation by activated oxygen species due to impairment of the electron transport in plants (Zhang and Kirkham, 1994). It is suggested that lipid peroxidation is much lower in sorghum and occurs later in the drought stage compared to other crops (Zhang and Kirkham, 1994).

Leaves and stems of many sorghum varieties are covered with a waxy bloom substance. This is an adaptation for drought avoidance. The cuticle and epicuticular wax structure and composition determine the hydraulic permeability of the leaf. Most cultivated sorghum genotypes have a close to maximum epicuticular wax (Jordan et al., 1983).

Under water stress, leaves of sorghum can become erect and roll. This result in a decreased leaf surface area exposed to incoming solar radiation and decreases water loss. A delay in growth and development and quick recovery after stress was reported by Sanchez-Diaz and Karmer (1971). Lower leaves in the canopy and older leaves can senesce during water stress that occurs during grain filling and this also allows sorghum to maintain yield under severe stress.

WATER USE AND DROUGHT RESPONSE VARIATION WITHIN SORGHUM GENOTYPES

Variation in water requirement within plant species, and specifically in sorghum, was reported by Briggs and Shantz (1913). Other researchers have also shown differences in water use among grain sorghum by directly comparing water use of different sorghum cultivars and their yield (Garrity et al., 1982a; O'Neill, 1986) or indirectly through measuring differences in gas exchange between hybrids (Saranga, 1990).

Similarly, drought response variation among sorghum hybrids is evident. The existence of variation in yield among sorghum hybrids is the long term base for breeding programs in dryland regions. A study reported grain yield variation of 184 g m^{-2} to 943 g m^{-2}, under drought stress, between sorghum hybrids (Blum et al., 1989). Variation in phenology, plant height, panicle, peduncle length, leaf area, and plant weight were also reported (Gangadhar, 1999; O'Neil et al., 1983).

Agronomic and physiological differences, i.e., osmotic adjustment (Tangpremsri et al., 1991); epicuticular wax content (Blum, 1988); leaf water potential; canopy temperature; leaf rolling; leaf carbon exchange rate; and stomatal conductance (Blum, 1989) are some of the reasons indicated for drought response variation between hybrids. Correlation between root variation and osmotic adjustment among sorghum genotypes was indicated (Tangpremsri et al., 1991). However, variation between roots of sorghum hybrids is less investigated than other aspects.

CONCLUSIONS

Crop water requirement is not as easy as determining the nutrient requirement of a crop because it is highly dependent on the environmental conditions. Therefore, it is often impossible to label a number as water requirement of a crop. Rather, a very wide range of numbers are suggested based on various experimental results to accommodate wide environmental conditions, hybrid differences, and their interactions. For maximum grain yield about 450-650 mm of water is required for grain sorghum. Most importantly, this amount of water should be well distributed depending on the crop stage of development and environmental demand, because yield is sensitive to water deficits at certain growth stages.

Numerous studies have attempted to address water stress and water stress effects in sorghum. From the approach of these studies alone, one can understand how complex the problem is. Some of the studies attempted to address water stress from the level of stress point of view (intensity), i.e., by imposing different levels water stress. Others attempt to study by imposing a stress for different lengths of time. Studies which attempted to study water stress based on different growth stages are also numerous. A factorial combination of these water stress effects were also studied. However, in practice water stress can happen in any complex combination. Therefore, there is no cure for avoiding stress than understanding the water requirement of sorghum and making sure our water resources are well distributed in required amounts at a given growth stage.

As is the case for many sorghum producers, if the total amount of water is not available, and water stress is expected, understanding that some growth stages of sorghum are more sensitive than others is important. Based on this knowledge one can optimize planting date or prioritize the irrigation scheme. Planting sorghum so that the growth stages with high water demand can fit with months where high rainfall expectation is one choice. The other choice is harvesting water and irrigating at those growth stages.

Hybrid differences can play a role, if it is not possible to select an early planting date. Selecting the best drought tolerant hybrid and employing the best management possible, i.e., optimum plant population, practicing no till, application of required nutrients and appropriate disease, pest, and weed control systems, one can meet the water requirement and narrow potential and actual yield differences in dryland production.

It is accepted that sorghum is more drought tolerant than other crops because of its root system, the ability to maintain stomatal opening at lower levels of leaf water potential than others, high osmotic adjustment, waxy bloom substance in leaves and stem, adjustment in leaf angle, and rolling in low water conditions. The existence of these variations among sorghum hybrids has also been observed. Therefore, selection of sorghum for drought tolerance should utilize this variation as a source in search for drought tolerant hybrids rather than only relying on yield alone.

Thus far, the focus of the majority of drought tolerant sorghum selections have focused on discovering cultivars that produce more grain from given amount of water, i.e., high WUE. Existence of variation and importance of WUE is undeniable. However, I believe that we will not eventually find or develop a hybrid that can produce a yield without water or nutrients. Therefore, the future focus should be finding a hybrid that efficiently recovers available water resource from the surroundings. For this reason, understanding root variations in sorghum should be well investigated and should be major component in development of future hybrids.

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Table 3.1. Yield-limiting factors and years as reported in Kansas State University grain sorghum performance trial reports (from 1957 to 2008).

Yield limiting factor	Years Reported
1. Abiotic factors	
Late-summer drought, August drought, Drought and high temperature, Hot dry weather, Hot dry summer, Heat and drought in July and August, Extreme growing season temperature, Above-normal temperature and below-normal rainfall	1960, 1962, 1963, 1964, 1965, 1966, 1967, 1968, 1970, 1972, 1973, 1975, 1976, 1978, 1980, 1983, 1984, 1987, 1988, 1989, 1990, 1991, 1994, 1997, 1998, 1999, 2000, 2002, 2003, 2006
Wet weather at harvest, Prolonged periods of mud snow and extreme cold conditions at harvest, Early frost, hail, Late-season storm, Sharp killing frost, High wind and early snow, Cool temperature at August and September	1961, 1964, 1967, 1972, 1981, 1982, 1985, 1989, 1992, 1993, 1995, 1996, 1997, 2004, 2005,
Wet weather at harvest, Extended rainfall at planting….	1961, 1973, 1978, 1982, 1983, 1984, 1992, 1993, 1995, 1999, 2001, 2007
Excessive rain, Lodging, Sprouting…………………….	1958, 1965, 1960, 1986, 1994, 1995, 2008
2. Biotic Factors	
Bird Damage……………………………………………	1959
Milo disease…………………………………………….	1962, 1966
Head smut, Borer in panicle, European corn borer, Corn borer, Corn leaf aphid, Spider mites, Yellow sugar cane aphid, Two spotted spider mite	1965, 1966, 1967, 1973, 1974, 1977, 1991, 1994, 1998, 2000, 2001, 2008
Earthworm, Midge, Sorghum midge, Corn earthworm, Armyworms, Fall armyworm, Headworms, Sorghum webworm, Cutworms, Wireworm, Grasshopper, Sugarcane rootstalk weevil, Caterpillar	1966, 1988, 1989, 1991, 1993, 1995, 1996, 1997, 1998, 1999, 2002, 2003, 2004, 2006, 2007, 2008
New biotype greenbug, Greenbug	1968, 1969, 1972, 1973, 1974, 1980, 1981, 1988, 1989, 1990, 1991, 1993, 1994, 1996, 1998, 2000, 2001, 2004
Chinch bugs, False chinchbugs, True chinch bugs	1977, 1978, 1980, 1981, 1988, 1989, 1990, 1991, 1993, 1994, 1996, 1998, 2000, 2001, 2003, 2004, 2007, 2008
Billbugs………………………………………………	1997, 1998, 2000, 2001
Maize dwarf mosaic, Maize mosaic Virus …………	1972, 1973, 1974, 1980,
Acremonium wilt, Sooty Strip, Sorghum downy mildew, Fusarium stalk rot, Charcoal rot, Stalk rot, Leaf blight, Bacterial strip, Rough spot, Rust streak, Fusarium head rot, Head smut, Crazy top, Head mold, Seedling blight (*Phythium* or *Fusarium*), Sorghum ergot, Rootless sorghum syndrome	1989, 1991, 1992, 1993, 1994, 1996, 1997, 1998, 1999, 2001, 2002, 2003, 2006, 2008

Chapter IV

Grain Sorghum Water Use, Morphology, and Physiology with Hybrid Advancement

ABSTRACT

Sorghum is a drought-tolerant crop, and its productivity in rainfed environments has increased since the 1950s. This increase is due to changes in agronomic practices and hybrid improvement. The objective of this study was to determine what aspects of grain sorghum morphology, physiology, and water use have changed with hybrid improvement and contributed to this yield increase. A 2-yr greenhouse experiment was conducted with five selected hybrids, one from each of the past five decades. The hybrids were studied in well-watered and pre- and post-flowering water stress conditions. Total water use, transpiration, stomatal conductance, and photosynthesis were measured during the growing period. Biomass and biomass components were measured at harvest. There was no consistent change in the leaf physiological parameters due to hybrid advancement. In contrast, total water use changed with hybrid advancement. The new hybrids used the greatest total water in the well-watered treatments and also had greater root-to-total biomass ratio than the old hybrids. Leaf biomass was also greater for the newest hybrid. Results indicated that hybrid development programs created hybrids with improved morphological characteristics that might have resulted in better resource use and ultimately to an increase in yield.

In the United States, grain sorghum yield has increased over the years, past five decades, at a rate of approximately 50 kg ha^{-1} $year^{-1}$ (Eghball and Power, 1995). The increase in sorghum productivity is due to changes in agronomic practices and hybrid improvement (Assefa and Staggenborg, 2010). Approximately 35 to 40% of the total yield gain in grain sorghum is believed to be a result of hybrid improvement. Approximately 60 to 65% of the yield gain is due to changes in cultural practices like nitrogen fertilizer, irrigation, and tillage (Duvick, 1999).

Hybrid improvement in grain sorghum, which is usually measured in terms of yield, is a result of improvement in disease resistance, herbicide resistance, drought tolerance, and improved nutrient and water use. These genetic improvements are associated with and manifested in the plants phenology, physiology, phenotype, and phenotypic traits.

Sorghum's water use, morphology, and physiology make it more drought-tolerant than other crops. For example, sorghum has a lower water requirement and twice as many secondary roots per unit of primary roots than corn (Martin, 1930). These root characteristics, the ability to maintain stomatal opening at low levels of leaf water potential, high osmotic adjustment, waxy bloom substance on leaves and stems, and adjustment in leaf angle and leaf rolling with low water availability enable grain sorghum to tolerate drought better than many other cereal crops (Johnson and Turner, 1978; Machado and Paulsen 2001; Turner, 1974). Therefore, changes in sorghum yield due to hybrid improvement could also be explained by changes in plant morphology and physiology.

Several studies have compared old and new maize hybrids to determine what factors contributed to a yield increase over time (Tollenaar, 1991; Duvick, 2005). Studies have also compared old and new wheat hybrids to investigate factors that contributed for yield increase over years (Calderini, 1994). These studies, in corn and wheat, were accomplished by selecting hybrids each representing past decades. Yet, few researches have conducted a similar study in sorghum. Mason et al. (2008) studied yield components of corn and sorghum over years and concluded that yield increases in corn was resulted from an increase in one yield component (ear m^{-2}) but yield increases in sorghum were not related to yield components. Therefore, the cause of increase in sorghum yields due to hybrid improvement still remains a research gap.

The main objective of this study was to test the hypothesis that the genetic contribution to yield improvement in sorghum hybrids can be explained by changes in water use, morphological, and physiological traits that were deliberately or inadvertently introduced during hybrid improvement. To test this hypothesis a greenhouse experiment was conducted on five sorghum hybrids, one from each of the past five decades.

MATERIAL AND METHODS

Greenhouse experiments were conducted from May to September in both 2007 and 2008. The greenhouse temperature was maintained at about 27°C day and 21°C night in both years. Experimental treatments were five sorghum hybrids and three watering schedules. The five hybrids used in the 2007 experiment were P848, P828, P8585, P8358, and P85G46. In 2008, seeds of RS610 and P833 were not available and were replaced with P848 and P828, respectively. These hybrids were selected to represent hybrids released during the periods 1954-1964, 1964-1974, 1974-1984, 1984-1994, and 1994-2005. Within their respective release periods, these hybrids had average to above average yields and were of similar maturity (Kansas State University, 1957-2008).

Watering treatments were a well-watered control, pre-flowering water stress, and post-flowering water stress. The well-watered plants were watered to 75% of field (pot) capacity every 3 to 5 d. The pre-flowering water stress treatment occurred from growing point differentiation to half-bloom, and the post-flowering watering stress occurred from half bloom to harvest. To achieve water stress, water was withheld until leaf rolling was observed, before adding water to field capacity. The design of the experiment was a factorial complete randomized design. Each treatment (hybrid X watering) was randomly assigned to pots and replicated three times each year.

Plants were established in 50 cm deep pots with a volume of 26.4-L pots (Poly Tainer basket; Hummert Supply, St. Louis, MO). To prevent water leakage from the pots, the bottom inside of each pot was covered with aluminum foil in 2007 and lined with a plastic bag in 2008. The growing media was soil, sand, and peat mix (1:1:2 volume ratios). Water holding capacity of this soil was determined by weighing the soil before and 12 h after saturation with water. Before sowing, about 2.3 g of fertilizer (OSMOCOTE Classic, Control release fertilizer, 14-14-14; Scotts-Sierra Horticultural Products Company, Marysville, OH) was added and mixed with the soil. Three seeds were sown per pot, and thinned to two plants per pot at approximately the two-leaf stage.

After sowing, pots were watered to 75% of field (pot) capacity. Pots were weighed, and subsequent watering was determined by weighing the pot and adding enough water to replace the lost water. The total water applied to each pot at harvest was calculated by adding the amount of water applied at each application time to compensate for lost water. The water lost from a pot was assumed to account for losses via evapotranspiration (ET).

Leaf temperature (LT), stomatal conductance (g_s), photosynthesis (Pn) and transpiration (T) of the last fully expanded leaf were measured at 43, 47, 49, 54, 56, 62, 64, 67, and 71 days after planting (DAP) with a portable photosynthesis system (LI-6400, LI-COR Inc., Lincoln, NE, USA) in 2008. In 2007 and 2008, plant height and panicle length were measured just before harvest. In 2008, peduncle length was also measured. Plant height was measured from the soil line to the top of the panicle. Panicle length was measure from base to apex of the panicle. Peduncle length was measured from attachment of the flag leaf on the stem to the base of the panicle.

At harvest, aboveground biomass was collected just above the soil line, and stem, leaf, and panicle were separated. Roots were carefully separated from soil by washing and detached roots were trapped on a wire screen. Biomass components were oven dried at 60°C for 4 d and dry weights were recorded. Grain yield was measured after drying the panicle and hand threshing the caryopses for weighing.

Common data from the 2007 and 2008 experiments were analyzed with years as replications. Time-series data (water use, LT, T, g_s, and Pn at different DAP) were analyzed as repeated measures by using the PROC GLM procedure of SAS (SAS Inst., Cary, NC, 2001) for effects within and between variables. Total water, biomass and biomass components of hybrids in different watering treatments were analyzed using the PROC GLM procedure of SAS. For significant variables, mean separation was accomplished using Duncan's multiple test. The relationship between total water applied and biomass and grain yield and relationships between LT, T, g_s, and Pn were analyzed using the PROC REG procedure of SAS.

RESULTS AND DISCUSSION

Daily and Total Water Use

A repeated measure analysis of the water use data reported a difference in water use measured at different DAP. The interaction between water treatment and days also was significant. No differences in water use among hybrids or interactions between hybrids and days were measured. Separating water use into different DAP found that there was no difference in water use between the water treatments during the first 45 DAP (Fig. 4.1). There was likely no differences in water use during this time period because there were no treatment differences until approximately 30 DAP.

Hybrids water use increased from about 100 to 300 cm^3 in the first 45 DAP to 900 to 1200 cm^3 from 45 to 60 DAP. There was a difference in water use between watering treatments in this time period (45-60 DAP). Obviously, hybrid water use in the pre-flowering water stress treatments was lower than that in the well-watered control and post-flowering stress treatments because water was withheld during this time period (45-60 DAP).

Water use declined after about 60 DAP for all hybrids and in all water treatments. Water use from approximately 60 DAP to maturity was lowest for the post-flowering stress treatments and highest for the pre-flowering stress treatments. The lower water use for the post-flowering water stress treatment is due to water withheld during this time period. Plants in the pre-flowering stress treatment likely used more water during this time period because they resumed growth when watering resumed after stress.

The interaction between hybrid and watering treatment was significant for total water applied (Table 4.1). Total water applied in the well-watered control treatment increased with hybrid advancement (i.e. greater for new hybrids than for old hybrids, Fig 4. 2a). Total water applied in pre- and post-flowering stress treatments, however, was not different between hybrids. The differences in total water between hybrids in well-watered treatments occurred because of the application of water to maintain field (pot) capacity, i.e. the more water lost the higher application. Apparently, recently released hybrids used more of the available water in the soil better than the older hybrids.

Our results for daily water use of sorghum hybrids agree with previous reports. Early in the growing season, the average daily water use of sorghum low. The water requirement then increased from approximately the seven-leaf stage until the boot stage. Maximum daily water use occurred from the boot stage until after anthesis, which fits the period from 40 to 60 DAP in our study. The daily water requirement then decreased during grain fill as the crop began to senesce (FAO, 2002). The negative effect of water stress on daily water use due to reasons such as reduced stomatal conductance is evident from many other studies (Cechin, 1997; Salih et al., 1999; Subramanian and M Maheswari, 1989). To our knowledge, no studies have tried to relate hybrid improvement of sorghum with daily or total water use changes; however, research has directly and indirectly shown differences in water use among grain sorghum hybrids (Garrity et al., 1982a; Saranga, 1990).

Water, Biomass, and Grain Yield

The interaction between hybrid and watering treatment was significant for total biomass production (Table 4.1). In the well-watered treatment, the greatest biomass was obtained from the newest hybrid in the experiment (Fig. 4.2b). There was no difference in total biomass production between hybrids within the pre- and post-flowering stress treatments. Hybrids in the stress treatments had less overall biomass production than hybrids in the well-watered treatment.

There was a positive, linear relationship between the total water applied and total biomass produced (Table 4.2) regardless of treatment differences. A regression analysis of biomass and total water in individual hybrid responses, irrespective of watering treatments, found that new hybrids had more biomass per total applied water (Fig. 4.3). Similarly, a regression analysis of biomass and total water, irrespective of hybrid differences, revealed a stronger relationship for well-watered treatment alone than for all watering treatments considered together (Table 4.2). The relationship between biomass and total water was weak for the post- and pre-flowering stress treatments than for the control.

Water treatment and hybrids affected sorghum grain yield (Table 4.1). The interaction between hybrid and watering, however, was not significant. Grain yield was greater in the well-watered control treatment than in either stress treatment. There was a 25% decrease in grain yield due to pre- and post-flowering water stress. Overall the greatest grain yield was obtained from the two newest hybrids and the oldest hybrid. Grain yield increased from the second-oldest hybrid towards the new hybrids.

Taking all treatments together, there was no significant linear relationship between total applied water and grain yield production (Table 4.2). However, considering the well-watered treatment alone generated a better positive linear relationship between total water and grain yield. There was no linear relationship between grain yield and total water in the pre-and post-flowering stress treatments or when they were included in the data set (data not shown).

These results agree with previous research results. A linear relationship between sorghum biomass and ET was reported previously (Hanks et al., 1969; Inuyama et al., 1976). Unlike biomass, the relationship between grain yield and water is complex because it is sensitive to water deficits at certain growth stages (Garrity et al., 1982b). Therefore, grain yield is more dependent on rainfall or irrigation distribution over the growing season than on total water available through the growing season. Howell and Hiler (1975) found that yield response of grain sorghum was not strongly correlated to seasonal ET but was highly dependent on timing of the ET deficit.

Treatment Effect on Biomass Components

Hybrid differences affected root biomass (Table 4.1). Root dry weight increased with hybrid advancement. The hybrid improvement program is designed in steps: (1) create hybrid from parents that have traits of interest, (2) evaluate hybrids in multiple years and locations, and (3) release superior hybrids. Testing in multiple years and locations in more dryland areas than irrigated areas might have favored continuous improvement of hybrids that have better root biomass which increased use of available water resource. Our results agree with those of Campos et al. (2004), who observed a difference in root water extraction by old and modern maize hybrids. They reported that old hybrids extracted more water from a shallow depth, whereas modern hybrids extracted water from deeper depths. This also explains why new sorghum hybrids in the present study had a higher total water use in the well-watered control treatment.

Neither the water treatments nor the interaction of hybrid with watering treatment were significant for root biomass production. This indicates that grain sorghum reduces its aboveground biomass (e.g., grain yield and plant height) in the presence of water stress but not its root biomass. This is in agreement with the findings of Salih et al. (1999) and Younis et al. (2000), who reported that root growth was unaffected by water stress.

Leaf dry weight was different between hybrids (Table 4.1). The greatest leaf dry weight was obtained from the newest hybrid, P85G46, and the mid era hybrid, P8585. There was no difference between leaf weights of the rest of the hybrids. Leaf weight also was not different between water treatments, and there was no interaction between hybrid and water treatment on leaf weight. Our observations indicate the increase in leaf area, rather than leaf number, is the factor that contributed for higher leaf weight for hybrid P85G46. Duvick (2005) concluded that there was no change in leaf area index or leaf number with corn hybrid advancement in the USA, but Tollenaar, (1991) reported a change in leaf area index with corn hybrid advancement in Canada

Panicle weight and length were different between water treatments and hybrids (Table 4.1). . The interaction between hybrid and watering treatment was not significant for both panicle weight and length. Panicle weight results were similar to grain yield because of a strong linear relationship between the two parameters (R^2=0.96). Panicle weight was greater in the well-watered control than in both stress treatments. Overall, the greatest panicle weight was obtained from the newest hybrid. There was no strong association between panicle length and grain yield obtained. Panicle length of hybrids in the pre-flowering water stress treatment was shorter than the well-watered and post-flowering stress treatments. The three newest hybrids had longer panicles than the two oldest hybrids.

Changes in panicle weight and length with advancement of sorghum hybrids are seldom reported. However, variation between sorghum hybrids in panicle weight and length; a similar association of these biomass components with grain yield reported in the present paper; and a similar effect of water stress in panicle length and weight have been reported by other researchers (Ayana and Bekele, 2000; Beil and Atkins, 1967; Craufurd, 1993; Ezeaku and Mohammed, 2006).

The interaction between hybrid and water treatment was significant for peduncle length, which was measured only in the 2008 experiment (Fig. 4.2c). In the well-watered and post-flowering stress treatments, peduncle length decreased from the oldest to the newest hybrid. All hybrids had a shorter peduncle in the pre-flowering water stress treatment than in well-watered and post-flowering stress treatments; however, within the pre-flowering treatment, the newest hybrid had a longer peduncle than the other hybrids.

Plant height differed between water treatments (Table 4.1). There was no height difference between plants in the well-watered control and post-flowering stress treatments, but plants in pre-flowering stress treatment were shorter than those in two other treatments. This illustrates the tendency of sorghum to reduce growth in vegetative or pre-flowering water stress and resume growth when the stress is relived. There was no difference in height between hybrids.

Water Use and Physiology

There were significant differences between hybrids, watering treatments, and DAP for T, g_s and Pn (Table 4.3). The interaction between watering and hybrid was not significant. The interaction between watering treatments and DAP was significant for LT, T, g_s, and Pn (Fig. 4). The well-watered treatment had greater T, g_s, Pn and relatively cooler LT than the pre-flowering stress treatment from 43 to 62 DAP. At 62 DAP, all watering treatments had the lowest LT, T, g_s, and Pn. The low LT, T, g_s, and Pn on this day were due to cloudy weather. From 62 to 71 DAP the well-watered and pre-flowering stress treatments (which were not under stress at this time) had the greater T, g_s, and Pn and cooler LT than the post-flowering stress treatment. This shows that hybrids had less T, g_s, Pn, and relatively warmer LT when they were on water stress.

Of the five hybrids, the oldest had the highest T and g_s and lowest LT. Hybrid P8585, which represented the middle decade in this experiment (1974-1984), had the lowest T and G_s. Therefore, there was no positive or negative trend in LT, T, or g_s with hybrid advancement. Photosynthesis was the highest for the oldest and the two new hybrids. There was also no significant trend in Pn with hybrid advancement.

A positive correlation between T, G_s, and Pn was reported previously (Jarvis and Davis, 1998; Wong et al., 1979). The negative effect of water stress on T, gs, and Pn and an increase in LT due to stomatal closure also agrees with previous reports (Kaori et al., 2009). Unlike the result from our experiment, a conclusion from comparison of leaf Pn between old and new corn hybrids showed that Pn was more efficient in new hybrids than older hybrids when compared in range of stress conditions. Similarly, greater transpiration and cooler canopy temperature characterized new corn hybrids compared with old hybrids in drought stress conditions (Duvick, 2005). The discrepancy between our results and the conclusions in corn hybrids might be explained on the type of experiments the conclusion draw upon. In a field experiment, we expect a similar, higher photosynthesis and transpiration and cooler leaf temperature in new sorghum hybrids than old hybrids, since the new hybrids have higher root biomass to explore the available water resource.

A similar explanation works for why grain yield in the present study did not show a consistent increase with years of release as reported by different authors (Eghball and Power, 1995; Unger and Baumhardt, 1999; Assefa and Staggenborg, 2010). All the increase in sorghum yield with advancement of hybrids reported previously was drawn from field experiments. However, the present research was in a greenhouse, where we captured differences in hybrids under controlled resource supplies. Results in the present research suggest a difference in total water use perhaps due to changes in morphology, like increased root biomass, was responsible for increased yield in dryland with advancement of sorghum hybrids reported by others.

CONCLUSIONS

1- Sorghum water use during the growing season was different at different days from planting. Periods of water stress resulted in decreased water use in all hybrids. Daily water use was not different between hybrids, but total water use was higher for new hybrids than old hybrids.

2- Total (shoot + root) biomass accumulation and grain yield were greater in the well-watered treatment (when water was no limiting) than with water stress conditions. In the well-watered treatments, biomass was greatest in the new hybrids.

3- Overall, greater root and panicle weight contributed to the increase in biomass with hybrid advancement. Root biomass showed a consistent increase with hybrid advancement. Panicle weight was greater for new hybrids than for old hybrids. Leaf biomass also was greatest for the newest hybrid and the mid-era hybrid.

4- There was no difference in total height of the tested hybrids. However, panicle length of the newer hybrids was longer than that of the two oldest hybrids. The interaction between hybrid and water treatment was significant for peduncle length. In the well-watered treatment, peduncle length decreased with hybrid advancement.

5- There was no positive or negative trend in LT, T, g_s, and Pn with hybrid advancement. Hybrids exposed to water stress had lower T, G_s, Pn, and relatively higher LT than hybrids in the well-watered treatment.

On the basis of these results, we concluded that grain yield changes with hybrid improvement could have occurred through deliberate or inadvertent selection of hybrids with improved morphological characteristics. These changes were mainly increases in root, panicle, and leaf biomass and a decrease in the peduncle-to- panicle length ratio that could have enabled greater and efficient use of available resources.

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Table 4.1 Effect of hybrid differences, watering treatments, and their interaction on biomass, grain yield, dry weight of; root, leaf stem and panicle, length of panicle and plant height.

Treatment	Total water	Biomass	Grain yield	Root dry weight	Leaf dry weight	Stem dry weight	Panicle dry weight	Plant height	Panicle length
Hybrids	$m^3 pot^{-1}$			g plant^{-1}					cm
P848/RS610	0.026	49.3	16.9ba†	6.7c	9.4b	13.9	18.8b	97.5	19.9b
P833/ P828	0.027	51.5	13.1b	9.2bc	9.7b	16.6	15.4b	100.9	18.7b
P8585	0.026	51.6	13.5b	11.6ba	10.6ba	13.3	16.1b	90.0	23.6a
P8358	0.027	57.4	16.6ba	12.5ba	10.4b	15.6	18.9b	96.9	23.6a
P85G46	0.029	67.0	21.1a	15.1a	12.4a	15.3	24.2a	97.6	23.5a
Water	$m^3 pot^{-1}$			g plant^{-1}					cm
Well-watered control	0.029	60.9	19.8a	12.4	10.8	15.3	22.2a	101a	22.6a
Pre-flowering stress	0.026	52.5	15.2b	10.4	10.5	14.2	16.8b	83b	20.1b
Post-flowering stress	0.025	52.7	13.7b	9.9	10.2	15.4	17.1b	103a	22.9a
Effect					Pr>F				
Hybrid (H)	0.01	0.01	0.01	0.01	0.03	0.07	0.01	0.43	0.01
Watering (W)	0.01	0.01	0.01	0.26	0.73	0.41	0.01	0.01	0.03
W*H	0.01	0.04	0.26	0.26	0.65	0.29	0.14	0.61	0.91

†Within columns, means followed by same letter are not significantly different at $P \leq 0.05$

Table 4. 2 SAS system REG procedure output for model with dependant variables of biomass and grain yield and independent variable of total water

Relationship between	Variables	Parameter Estimate	Standard Error	Pr>|t|	R^2
Biomass and total water (all treatments)	Intercept	-32.4	8.9	0.01	0.49
	Total water	3233.1	326.6	0.01	
Biomass and total water in well-watered	Intercept	-63.5	15.5	0.01	0.67
	Total water	4237.6	522.9	0.01	
Grain yield and total water (all treatments)	Intercept	-2.8	7.0	0.69	0.07
	Total water	704.1	256.5	0.01	
Grain yield and total water in well-watered	Intercept	-24.3	10.3	0.02	0.37
	Total water	1511.8	347.0	0.01	

Table 4. 3 Effect of hybrid differences, watering treatments, days from planting, and their interaction on leaf temperature (LT), stomatal conductance (g_s), transpiration (T) and Photosynthesis (Pn).

Treatments	Leaf temperature	Stomatal Conductance	Transpiration	Photosynthesis
	^oC	mmol m^{-2} sec^{-1}	mmol H_2O m^{-2} sec^{-1}	µmol CO_2 m^{-2} sec^{-1}
Hybrid				
P848/RS610	31.75b†	1.04a	14.11a	68.79a
P833/ P828	32.04a	0.80b	11.92b	62.12bc
P8585	32.10a	0.62c	10.58c	58.36c
P8358	32.00a	0.78b	11.66b	63.67bc
P85G46	32.00a	0.79b	12.14b	66.56ba
Water				
Well-watered control	31.89	0.86	13.15	69.22
Pre-flowering stress	32.01	0.76	11.73	60.09
Post-flowering stress	32.03	0.80	11.36	62.39
Days After Planting (DAP)	**	**	**	**
Hybrid (H)	**	**	**	**
Watering (W)	NS	**	**	**
WxH	NS	NS	NS	NS
WxDAP	**	**	**	**
HxDAP	NS	NS	NS	NS
HxWxDAP	NS	NS	NS	NS

†Within columns, means followed by same letter are not significantly different at $P \leq 0.05$

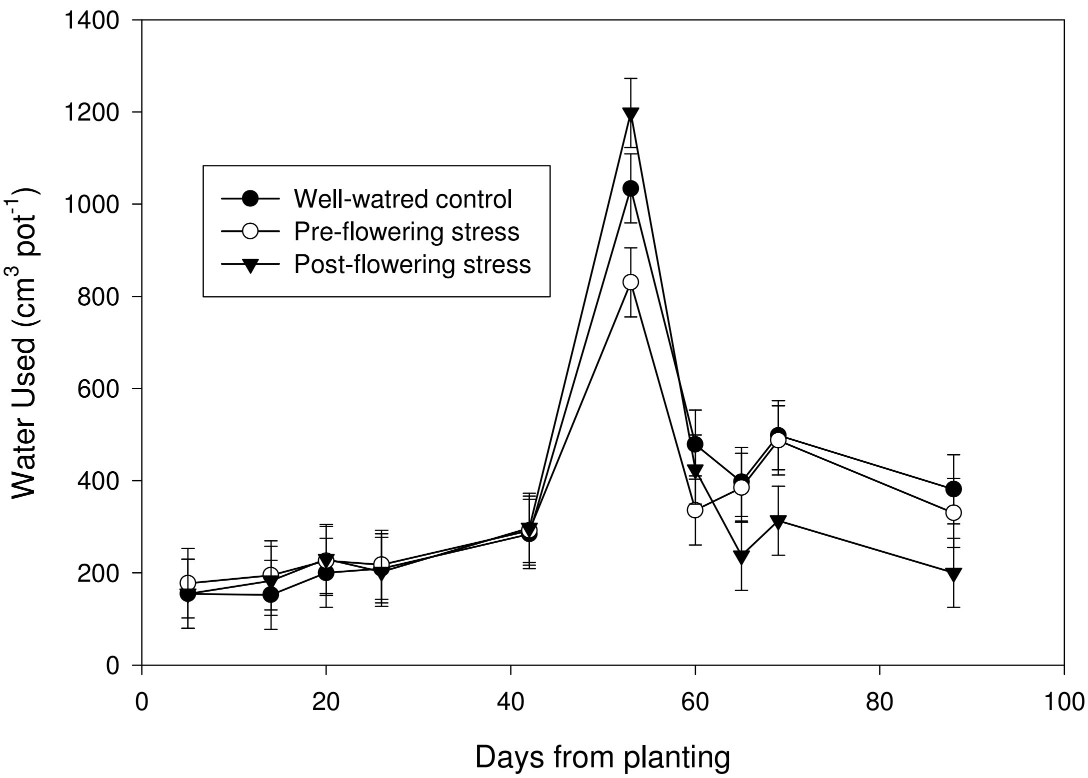

Figure 4.1 Daily water use of hybrids in three different water treatments: well-watered, pre-flowering stress, and post-flowering stress.

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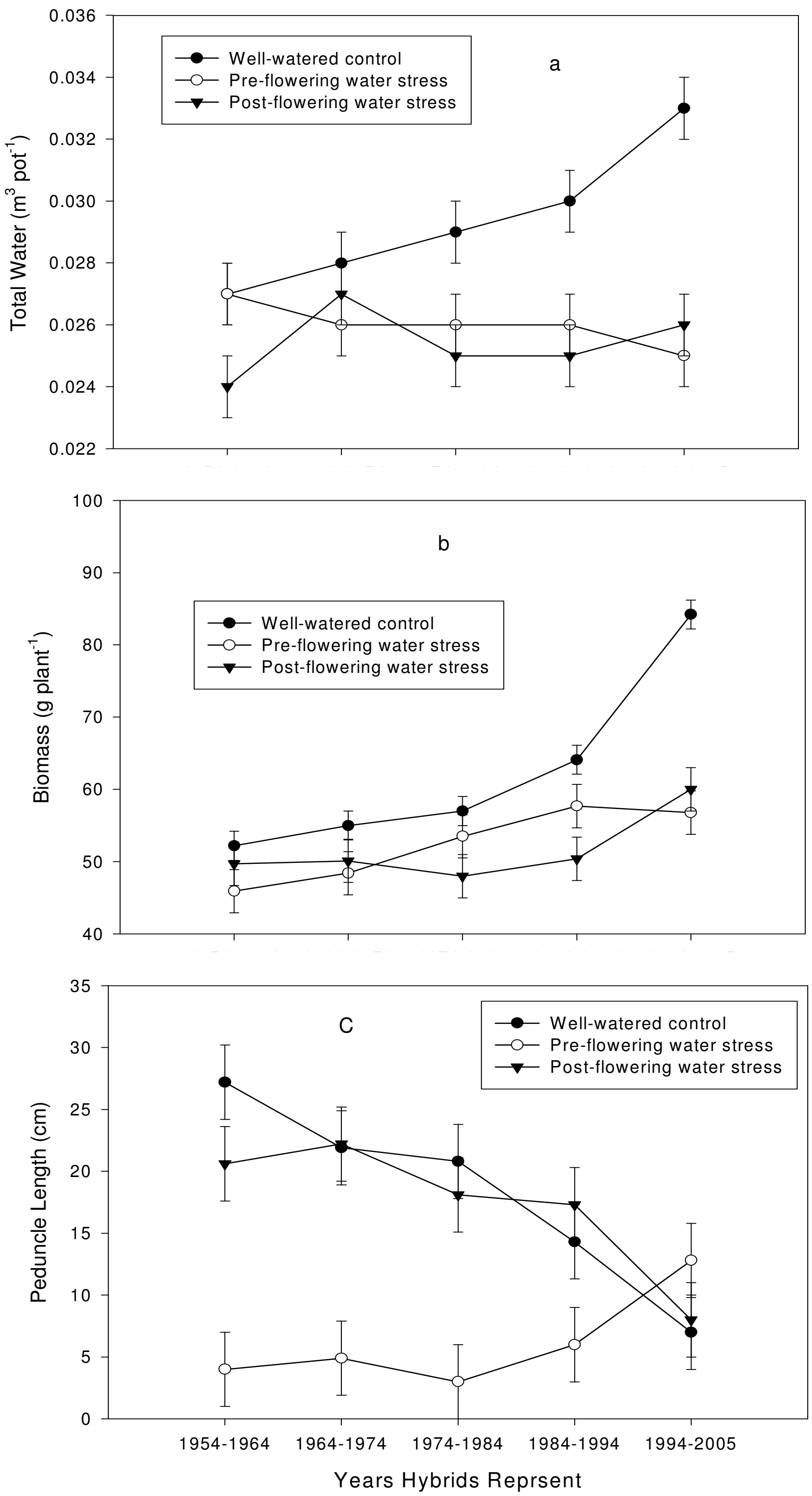

Figure 4.2 The interaction of hybrids and watering treatments on; (a) total water use, (b), total biomass (shoot + root), and (c) Peduncle length.

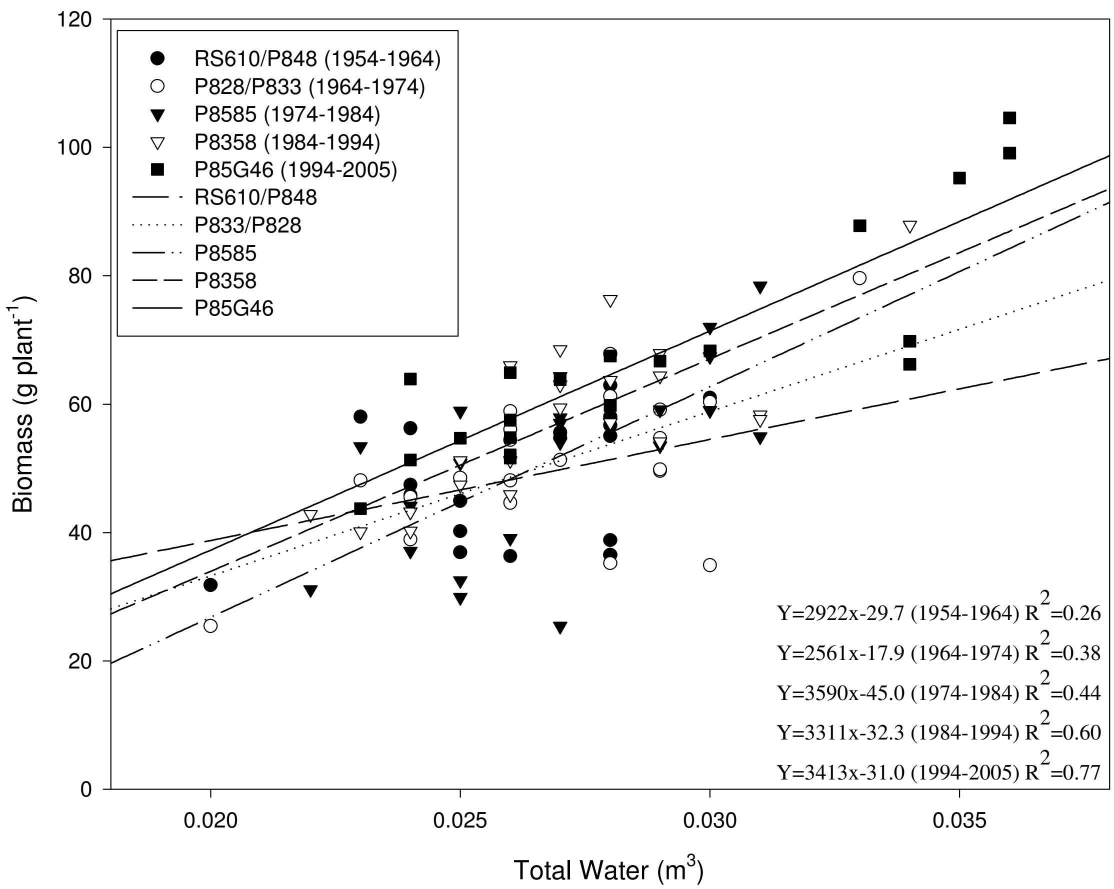

Figure 4.3 Relationship between total biomass (shoot + root) and total water applied for five different hybrids. Data from well-watered, pre-flowering, and post-flowering water stress treatments were combined for each hybrid.

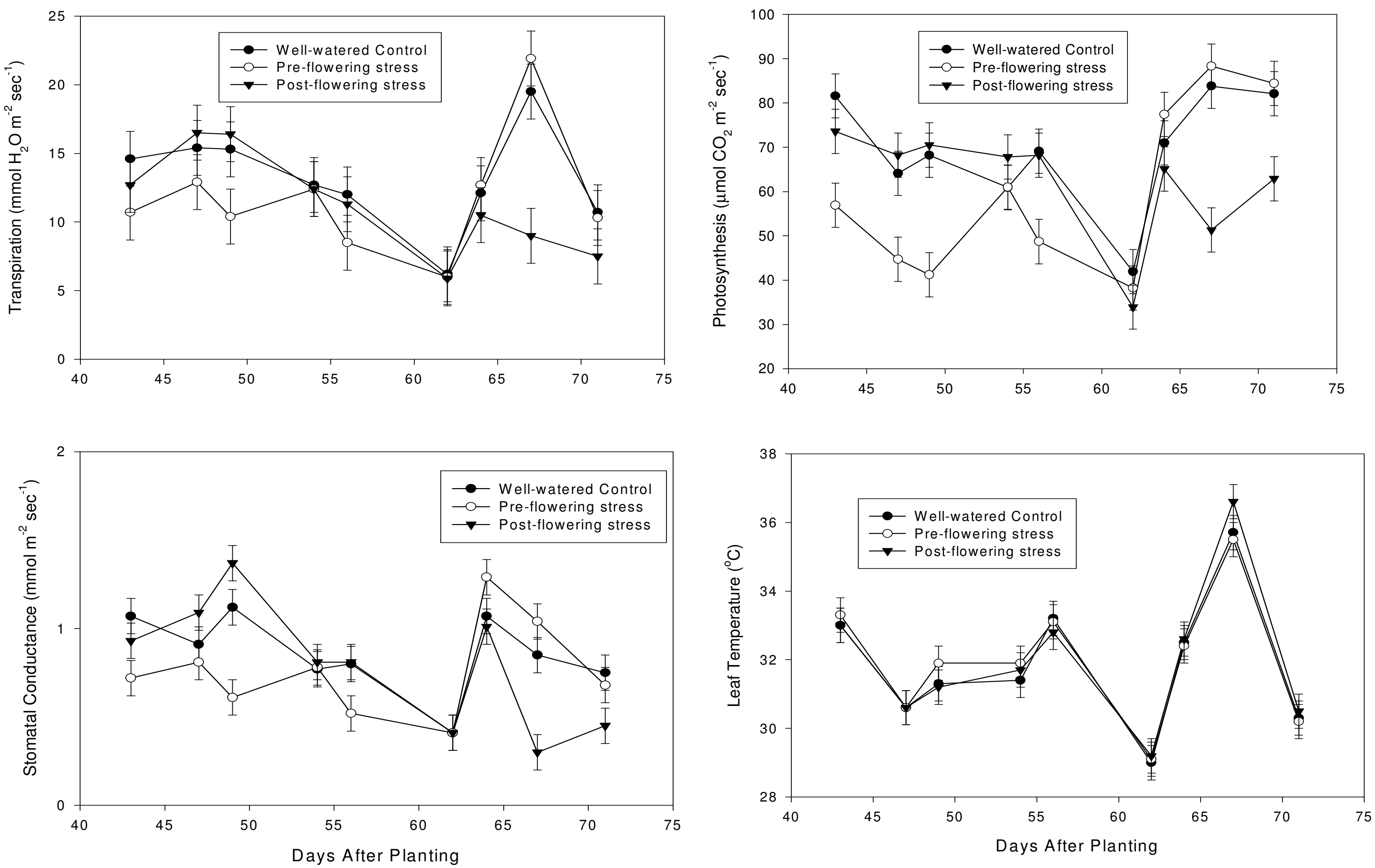

Figure 4.4 Effect of watering treatments on transpiration, stomatal conductance, photosynthesis, and leaf temperature with all hybrids combined.

Chapter V

Grain Sorghum Requirement of Primary Nutrients: A Review

ABSTRACT

A satisfactory sorghum yield requires availability of nutrients in a required amount and at the appropriate time. Low or excess nutrient application would not be economically nor ecological sound. Therefore, understanding the nutrient requirement and basis for fertilizer recommendations in sorghum production is crucial. The objectives of the present review was to understand the primary nutrient requirements, fertilizer recommendations, genotypic variation (in nutrient use) in grain sorghum and to suggest possible management options that would increase nutrient use efficiency and grain sorghum yield. Reports of more than sixty papers from peer reviewed journals, extension publications, and web pages were reviewed. Results suggest that grain sorghum yielding 9 Mg ha^{-1} takes up approximately 250 – 280 kg N ha^{-1}, 80 – 100 kg P ha^{-1}, 250 – 320 kg K ha^{-1}. Fertilizer recommendation for these primary nutrients in sorghum production is mainly based on soil test values. However, fertilizer recommendations vary based on yield goal, previous crop, organic matter content of soil, price of crop, and price of the fertilizer, in addition to soil test values. Studies pointed out different management factors that would affect nutrient availability and uptake by sorghum. Results also suggested existence of genotypic variation in nutrient uptake and allocation to different tissues among hybrids of sorghum. With the review, possible management options and research gap were identified.

A satisfactory crop yield requires availability of proper nutrients to the growing plant. Studies indicate that commercial nutrient inputs contributed about 30 to 50% of crop production in the USA (Nelson, 1990; Stewart et al., 2005). However, this value varies from crop to crop. Smith et al. (1990) studied the impact of eliminating chemical inputs from different crop production system and reported a yield reduction of 41, 37, 27, 19, 19, 16, 0, and 0% in corn, cotton, rice, barley, sorghum, wheat, soybean and peanut production, respectively.

From 1960 to 2007, the consumption of N, P, and K fertilizer in the US increased by 4.5, 1.7, and 2.3 folds, respectively (USDA ERS, 2009). Within the same timeline, sorghum yield increased significantly. A study reported that about 34% of sorghum yield increase from 1957 through 2008 was due to increased N fertilizer use (Assefa and Staggenborg, 2010).

Application of the right amount nutrient at the right time would result a significant yield gain, as indicated above. However, excessive or untimely application would have a negative impact to the sorghum plant as well as the environment (Kremser and Schnug, 2002). In addition, reports indicate that sorghum fertilizer use efficiency is less than 50%. However, this value could increase with proper management and selection of efficient genotypes based on nutrient uptake studies. Therefore, information on nutrient requirements of a crop, genetic variability for nutrient uptake, and management factors that might increase fertilizer use are useful to determine bases for fertilizer recommendation.

The objectives of the present review was to understand the primary nutrient requirements of sorghum, fertilizer recommendations for grain sorghum, genetic variations in nutrient use and translocation, and to suggest possible management options that would increase yield by increasing nutrient use. In order to attain these objectives, reports of more than sixty papers from peer reviewed journals, extension publications, and web pages were reviewed.

LITERATUR REVIEW

GRAIN SORGHUM NUTRIENT REQUIRMENT

Grain sorghum requires high levels of N and K and a reasonable amount of P for maximum yield. The need for secondary nutrients like calcium, magnesium and sulfur is moderate and micronutrients are needed in a small amounts.

Nitrogen is required by grain sorghum at all phases of development. About 250 – 280 kg N ha^{-1} would be taken up by irrigated sorghum yielding 9 Mg ha^{-1}. In early stages of growth, from planting to about 20 days after planting (DAP), N uptake is relatively low (Pal et al., 1982; Vanderlip, 1993). Nitrogen uptake increases in the log phase of sorghum growth and will be reduced near maturity. The maximum N uptake occurs between 30 to 75 day after planting. Sweeney and Moyer (2004) also reported that the maximum N uptake is between the nine-leaf stage and boot stage. With the same study, Sweeney and Moyer reported that uptake between the nine-leaf stage and boot stage is fourfold greater than nine-leaf stage. Nitrogen uptake declines between boot stage and soft dough stage.

Similarly, P is required by sorghum plants across the entire growing season. About 80 – 100 kg P ha^{-1} would be taken up by irrigated sorghum yielding 9 Mg ha^{-1}. Phosphorus uptake is low in the early growth stages, about 0 - 45 DAP. Most of the P in sorghum is absorbed late in the growing season, after 45 DAP through maturity (Srivastava, 1971). Roy and Wright (1974) reported a rapid increase in P uptake from 35 to 80 DAP. It is also reported that the highest percentage of P is taken up 21 to 60 DAP (Vanderlip, 1998).

The amount of potassium required by sorghum is the highest, i.e., about 250 – 320 kg K ha^{-1} would be taken up by sorghum yielding 9 Mg ha^{-1}. However, potassium deficiency is not as common as nitrogen and phosphorus in grain sorghum production. Potassium is important for stalk strength. Lack of potassium will result in lodging in sorghum. Potassium uptake by sorghum is rapid during early growth stages, 21-40 days from planting. At maturity, the major portion of K is contained in the vegetative tissue (Pal et al., 1982).

BASES FOR NUTRIENT RECOMMENDATION FOR GRAIN SORGHUM

NITROGEN

High nitrogen soil test levels resulted in an increased rate of carbon assimilation due to high investment of nitrogen in photosynthesis (Sugiyama et al., 1984). High N rates accelerate the conversion of rapidly synthesized carbohydrate in to protein. These results under luxuriant growth were finally expressed in high dry matter yield (Pal et al., 1982). Nitrogen deficiency, on the other hand, reduces sorghum leaf area, chlorophyll content, photosynthesis and often results in lower biomass and grain yield (Zhao et al., 2005).

Fertilizer recommendations for sorghum are mainly based on expected uptake by the crop and soil nitrate content. A study in North Carolina, USA, estimated that grain sorghum removes 15 mg of N kg^{-1} of grain and 10 mg N kg^{-1} of stover (Zublena, 1997). Based on this study, about 280 kg of N would be required for 8 Mg ha^{-1}grain yield and 16 Mg ha^{-1} stover yield.

A soil nitrate level above 20 mg kg^{-1} of soil, from 0 to 20 cm depth just before planting, could roughly be considered a level where no fertilizer application is required for grain sorghum production at any yield goal (Ferguson, 2000). Levels of nitrate less than 18 mg kg^{-1} of soil might be subject to different rates of fertilizer application based on other factors. Economic optimum N fertilizer recommendations usually consider; yield goal, organic matter content, N in the soil, previous crop, sorghum price, and fertilizer price (Mengel et al., 2003; Schlegel, 2000).

When inorganic N fertilizer is applied, it is not often fully utilized by sorghum. The reported average inorganic nitrogen fertilizer recovery rate for sorghum and other cereals is about 33% (Pal, 1983; Raun and Johnson, 1999). The remaining 67% of applied N would be lost from soil due to denitrification, surface runoff, volatilization, leaching, and released from the plant itself after anthesis (Harper et al., 1987). Improved soil and crop management systems can increase the inorganic N fertilizer use by sorghum.

PHOSPHORUS

Phosphorus is a component of nucleic acids and plays major role in biological energy transfer in plant cells. Therefore, it is vital for plant reproduction and growth. An adequate P supply for sorghum production would result in luxuriant crop growth and high grain yield (Ogunlela, 1988; Sahrawat et al., 1999).

Phosphorus deficiency in sorghum could lead to a significant decrease in grain yield. Therefore, application of P fertilizer is necessary based on available P in soil tests. Variation between soils exist, however, grain sorghum responds to applications of fertilizer if the soil test, in 0-20 cm depth, is below 15mg kg^{-1} $soil^{-1}$ by Bray-P1 and Mehlich-3 soil test or below 10 mg kg^{-1} $soil^{-1}$ by Olsen soil test (Wortmann et al., 2006). A yield goal based fertilizer recommendation by Kansas State University, USA, also shows that there is no need for phosphorus fertilizer applications for all yield goals (2.5 – 13 Mg ha^{-1}), if the Bray P1 test is above 20 mg kg^{-1} $soil^{-1}$ (Mengel et al., 2003).

In the soil, P is immobile mainly because it can be adsorbed to clay surface and organic matter or form complexes with iron and calcium. Therefore, the percentage recovered from applied phosphorus fertilizer is lower than N and it is only about 10 to 20% (Cooke, 1982). The remaining 80 to 90% of applied P will be adsorbed or precipitated depending on soil P level, clay and calcium content, and pH. Inside plants, however, P and N are both mobile. Therefore, in the case of deficiency, they will be translocated from old leaves and stem to actively growing leaves and to the head. At harvest, the highest percentage of P is found in the grain (Roy and Wright, 1974).

POTASSIUM

Potassium is believed to be involved in water, nutrient, and carbohydrate movement in plants. Adequate amounts of K in plant stimulate early growth, improve water use efficiency, improve resistance to disease and pest, and is vital to stalk strength or standability. Potassium uptake by grain sorghum and many plants is higher than all other nutrients. However, unlike N and P, potassium is not a yield limiting factor in many sorghum producing areas, because K is abundant in soils and in irrigation water. However, responses to K fertilizer application in sandy soils, poorly drained areas, and in areas with history of many years of crop production have been reported (Ferguson, 2000; Russell et al., 2006).

Different institutes have different K recommendation for grain sorghum. A soil test based fertilizer recommendation in Nebraska, USA, shows no need of K fertilizer if soil test K is above 125 mg kg^{-1} soil (Ferguson, 2000). Similarly, K sufficiency recommendation by Kansas State University, USA, also suggests no need for K application if exchangeable K (ammonium acetate extractable), is greater than or equal to 130 mg kg^{-1} soil for grain sorghum production (Mengel et al., 2003).

Similar to the variation in fertilizer recommendation, there is no consistent classification of soils based on K content for sorghum production. Many extension services in the United States would agree in grouping soils based on K content (in ammonium acetate extraction) as: very low K soils if 0-40 mg K kg^{-1} soil; low K soils if 41-80 mg K kg^{-1} soil; medium K soils if 81-120 mg K kg^{-1} soil; and high K soils if 120-160 mg K kg^{-1} soil; and very high if greater tan 160, for sorghum production as indicated by Gerwing (2005). A study from Venezuela grouped soils based on K content (in ammonium acetate extraction) as: low K soils if <24 mg K kg^{-1} soil; medium K soils if 24-57 mg K kg^{-1} soil; high K soils if 57-90 mg K kg^{-1} soil; and very high K soils if >90 mg K kg^{-1} soil, for sorghum production (Ramirez, 1989).

Like P, K in the soil is considered immobile. The amount of K released from organic matter via mineralization is insignificant. However, K could be held by organic matter in cation exchange. Therefore, the cation exchange capacity (CEC) of soil might be important to consider in K fertilizer recommendation. In few cases the higher the CEC the higher was the recommended fertilizer because it is considered that K will be adsorbed and become unavailable to plants (Beuerlein and Lentz, 2005; Kenneth, 2000). In other cases fertilizer recommendations decrease with increases in CEC because K losses through leaching in the high CEC soils would be lower than in low CEC soils.

FACTORS THAT INFLUENCE NUTRIENT AVAILABILITY IN GRAIN SORGHUM PRODUCTION

Water is a media in which nutrients dissolve; are transported from soil to root; and through which plant absorb them. Therefore, nutrient uptake by sorghum is highly dependent on soil available water. In other words, water stress can reduce nutrient uptake by roots and induce nutrient deficiency by decreasing the diffusion rate of nutrients from the soil to roots, by restricting transpiration rates, and impairing active transport and membrane permeability (Alam, 1999; Viets, 1972). A lower concentration of nutrients in sorghum during stress conditions compared with control treatments were reported by many authors (Eck and Musick, 1979; Rego et al., 1988).

Obviously, nutrient uptake and content of sorghum is highly dependent on availability of nutrient in the soil. The availability of nutrients in the soil depends on physical and chemical properties of the soil and soil management practices. Soil clay content, pH, and CEC are some of important factors that determine availability of primary nutrients in sorghum production. Grain sorghum is not tolerant to soil acidity, i.e., pH < 5.8 (Mask, 1988). Therefore, application of lime might be required in acidic soils. Clay content affects nutrient availability. Studies have shown that the response of sorghum to added P is less predictable from one soil to another (Sahrawat et al., 1995; Sahrawat et al., 1999).

In addition to the inherent soil nutrient content, the organic matter content of soil contributes to significant portions of N in sorghum production. Therefore, mineralization of soil organic N is often credited when determining N fertilizer application rates (Ferguson, 2000; Mengel et al., 2003). Soil and water conservation practices, which are geared toward decreasing soil erosion and leaching, would also increase fertilizer recovery by sorghum.

Research indicates that the higher the soil nutrient content or the higher the amount of nutrient applied, the higher is the uptake by sorghum. However, rates that exceed crop requirements would have adverse effect to plants and the environment. For example, the adverse effect of application of urea in excess amounts or in contact with seeds on germination has been reported (Brage et al., 1960, Hunter and Rosenau, 1965). Different reasons have been given for the adverse effects of urea on germination that include: impurities such as buiret and cynate, high pH from ammonium ion concentration, ammonia formed through hydrolysis of urea by soil urease, and/or formation of nitrite through nitrification. In addition, excess nutrients in soil might subject to leaching (Yadav, 1997) and result environmental problems.

Fertilizer application timing and application method can significantly affect grain sorghum nutrient uptake. Nitrogen for example, is a highly mobile nutrient both in the soil and in the plant. If the total required N is applied early in the season, a significant portion of it ca be lost through leaching. Therefore, split applications are recommended, i.e., starter fertilizer in band at planting and sidedress half application at about nine leaves stage (Khosla et al., 2000; Mostaghimi et al., 1991).

Tillage systems affect nutrient availability to sorghum and other plants. Intensive tillage accelerates mineralization of crop residue (Halvorson et al., 2001; Sainju and Singh, 2001) and could result in leaching. No-till systems might exhibit slower mineralization, greater N immobilization, denitrification, and ammonim volatilization (Rao and Dao, 1996; Philips et al., 1980; Rice and Smith, 1984).

Preceding crop and cover crops can also an effect nutrient availability in sorghum production. Sorghum can benefit from N contribution if planted after a legume or a cover crop (Bowen et al., 1986; Ebelhar et al., 1984; Sweeney and Mayer, 2004; Wortmann et al., 2007). Bagayoko et al. (1992) also indicated the advantage of soybean in rotation with sorghum over a continuous sorghum cropping system, in terms of N supply.

Grain sorghum uptake of nutrients from soil also depends on the plant population. Planting density is mainly dependent on water availability. However, it should also consider nutrient availability or should be coupled with increased level of nutrient application (Welch, 1966).

NUTRIENT UPTAKE VARATION AMONG SORGHUM HYBRIDS

Plants differ in their capacity to extract and absorb nutrients from the soil. The comparison of corn and sorghum in nitrogen uptake reveals the fact that the capacity of sorghum plants to take up nitrogen from soil was higher than maize in nitrogen limiting environments (Lemaire, 1996). A difference in the amount of nutrients translocated to different plant tissues between sorghum and corn was also reported (Jones, 1983; Perry and Olson, 1975).

Differences between varieties within species of plants in nutrient uptake ability are as great as differences in between species (Brown, 1979). Differences among hybrids of sorghum in nutrient use were reported by different authors (Maranville et al. 2002; Jacques et al., 1975). A study that compared tropical and U.S. origin hybrids reported similar uptake and allocation differences among sorghum genotypes (Traore and Maranville, 1999).

Unlike the reports in variation between nutrient use and allocation between sorghum genotypes, reports on factors behind these variations in nutrient use and allocation between sorghum are limited. Few of the studies available, however, reveled that root system development and rate at which a crop absorb a particular nutrient affects the total uptake and nutrient use of the crop (Lee et al., 1996; Rao et al., 1993).

CONCLUSION

Sorghum requires nutrients for healthy growth and development. The need for macronutrient, nitrogen, phosphorus and potassium is relatively high. Roughly, grain sorghum takes up about 250 – 280 kg N ha^{-1} , 80 – 100 kg P ha^{-1}, 250 – 320 kg K ha^{-1}, from soil to yield 9 Mg ha^{-1}. The uptake of these nutrients is at its peak from 20 to 70 days from planting.

The review found that soils that contain above 20 mg nitrate kg^{-1} of soil; 15 mg P kg^{-1} $soil^{-1}$ in Mehlich-3 test; and above 120 mg K kg^{-1} $soil^{-1}$ in ammonium acetate extraction, do not require N-P-K application for sorghum production. Soils with nutrient test levels less than these values, however, might result in fertilizer recommendations depending on factors such as the soil nutrient level, yield goal, organic matter content, CEC, previous crop, price of sorghum, and price of fertilizer.

Sorghum fertilizer nutrient use efficiency reported for the primary nutrients is well under 50%. This has negative implication from both the economic as well as from environmental point of view. However, proper crop management practices could increase this efficiency.

The nutrient uptake and content of sorghum depends mainly on availability of water; soil type; soil management factors; amount, time and method of fertilizer application; tillage practices; companion crops; and plant population. Variation among sorghum hybrids for uptake and allocation of nutrients was also evident.

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Chapter VI

Grain Sorghum Nutrient Uptake and Allocation with Advancement of Hybrids

ABSTRACT

In the USA, adoption and increasing use of sorghum hybrids occurred concurrently with increased use of inorganic fertilizer; both began in 1960. This occurrence obstructs attempts to use historical data to understand nutrient use and nutrient allocation patterns with sorghum hybrid advancement. The objective of this study was to determine nutrient use and nutrient allocation patterns of sorghum with hybrid advancement. Greenhouse experiments were conducted on five selected hybrids (one from each of the past five decades) fertilized with three N fertilizer application rates (0, 0.6, and 1.2 g N pot^{-1}). The dynamics of primary nutrient concentration in the soil water were analyzed from soil water samples taken every week after planting. The primary nutrient content of the soil, grain, leaves, stems, and roots was analyzed. Throughout the test period, there were differences in the concentration of nutrients in soil water because of different N application rates, but not hybrid differences. The soil nutrient content at harvest was also not different between hybrids. However, there was a difference in the amount of total nutrients extracted by hybrids, and there were differences between hybrids in allocation of nutrients to different plant parts. These results indicate that new hybrids can extract more primary nutrients than old hybrids, perhaps because of increased morphological characteristics that enable greater use of available resources.

The adoption and increased use of inorganic fertilizer and hybrid sorghum in the United States share the same historic timeline. From 1960 to 2007, consumption of N, P, and K fertilizer in the United States increased by 4.5-, 1.7-, and 2.3-fold, respectively (USDA ERS, 2009). Many improved sorghum hybrids were released over that same period. Sorghum hybrids were first available to farmers in 1957 and accounted for 90% of the planted sorghum area by 1960 (Smith and Frederiksen, 2000).

This overlap in fertilizer and hybrid adoption can be an impediment to separate the contribution of these two factors to sorghum yield improvements. For example, whether a result of coincidence of the same contribution by the two factors or confusion due to high correlation of these factors with years of analysis, Duvick (1999) and Smith et al. (1990) reported that sorghum yield is 19% higher than it would have been without the use of hybrids and N fertilizer, respectively.

Mean sorghum grain yields in the United States have improved from as low as 1.2 Mg ha^{-1} in the early 1950s to more than 3.5 Mg ha^{-1} in the early 21st century (Basra, 1999). From an analysis of 61 yr (1930-1990) of sorghum yield data, Eghball and Power (1995), reported a 50 kg ha^{-1} yr^{-1} yield increase in the United States.

Various agronomic and genetic factors contributed to this yield increase. According to Duvick (1999), approximately 35 to 40% of the total yield gain in grain sorghum is assumed to be due to hybrid improvement. Changes in cultural practices such as N fertilizer, irrigation, and tillage were assumed to be responsible for 60 to 65% of the yield gain. Unger and Baumhardt (1999) indicated that 1.5 Mg ha^{-1} of the 2.2 Mg ha^{-1} yield increase they reported was a result of increased soil water at planting due to changes in management practices; the other 0.7 Mg ha^{-1} was attributed to improved hybrids.

Studies have compared old and new corn hybrids to determine whether there is a differential reaction for different fertilizer amounts (Castleberry et al., 1984; Carlone and Russel 1987; McCulloogh et al 1994). Consequences of wheat breeding on N and P uptake by cultivars were also reported (Calderini et al., 1995). Reports on sorghum, however, fail to show nutrient uptake and partitioning characteristics of sorghum hybrids released in different years.

The objective of our research was to determine nutrient use and nutrient allocation patterns of sorghum with hybrid advancement. On the basis of the knowledge that drought tolerance is the factor that contributes most to increased sorghum yield and the fact that there was an increase in root and leaf biomass with hybrid advancement (chapter IV), we hypothesized that new hybrids have better nutrient uptake and allocation than old hybrids. The hypothesis was tested by conducting a greenhouse experiment on selected hybrids from the past five decades.

MATERIALS AND METHODS

Three greenhouse experiments were conducted in summer 2008, fall 2008, and summer 2009 to investigate nutrient use patterns and nutrient allocation with sorghum hybrid advancement. The greenhouse temperature was set at 27°C day and 21°C night in both years and maintained for the entire growing season. Treatments for the experiment were five sorghum hybrids and three N fertilizer rates.

The five hybrids used in summer and fall 2008 were Pioneer hybrids ‘RS610’, ‘P833’, ‘P8585’, ‘P8358’, and ‘P85G46’ (Pioneer Hi-breed Int. Inc., Johnston, IA). In summer 2009, ‘P848’ replaced RS610 because of seed availability. These hybrids were selected for the experiment because they (1) can represent release periods of 1954-1964, 1964-1974, 1974-1984, 1984-1994, and 1994-2005; 2) yielded average and above average during those release periods (Kansas grain sorghum performance test; 1956-2008); and (3) were of similar maturity.

Nitrogen application rates were 0 and 1.2 g N pot^{-1} in summer 2008 and 0, 0.6, and 1.2 g N pot^{-1} in fall 2008 and summer 2009. The experimental design was a split plot in which hybrids were the subplot (pots) and fertilizer rate was the main plot. Hybrids were replicated three times and completely randomized within a fertilizer rate. The main plots, fertilizer rate, were replicated over the three seasons.

Plants were established in pots (Poly-Taner-can, No. 5, Squat 12x10, HDPE Nursery Supplies Inc., Orange, CA). The growing media was soil, sand, and peat mix (1:1:2 ratio). The soil mix was placed in pots, and 2 g of diammonium phosphate (DAP) and N treatments were added as urea and mixed. Pots were watered to enhance seed-to-soil contact at planting. Three seeds were sown per pot, and plants were thinned to two plants per pot at approximately the two-leaf stage. Summer planting in both 2008 and 2009 was the last week of May, and harvest was the second week of September. In fall 2008, planting was the first week of October, and harvest was at the end of January 2009.

Soil water sampling was accomplished by placing a Rhizone soil moisture sampler (Ben Meadows Inc., Janesville, WI) approximately 10 cm deep in each pot. Soil water was collected from selected pots once a week starting at planting. To ensure there would be adequate soil moisture for sample extraction and that there was equilibrium between nutrients in the soil water and soil, pots were watered the night before sampling (8 to 12 h before sampling). About 10 ml of soil water was collected each week by creating a vacuum through a syringe. The samples were then analyzed for ammonium (NH_4-N), nitrate (NO_3-N), orthophosphorus (PO_4^{3-}), and potassium (K^+) concentration and pH.

At harvest, aboveground biomass was collected just above the soil line, and stem, leaf, and panicle were separated. Roots were carefully separated from soil by washing and detached roots were trapped on a wire mesh. These aboveground and root biomass components were oven dried at 60°C for 4 d, and dry weights recorded. Grain yield was measured after drying the panicle and threshing the caryopses from the panicle by hand. The amount of N, P, and K in each plant part was then determined by grinding each part separately and taking representative samples.

Soil samples were also collected before fertilizer application (before planting) and after harvest in each season. The three soil samples taken each season before planting were a representative of the soil used for all pots. Samples after harvest were taken from individual pots. All soil samples were analyzed for their ammonium (NH_4-N), nitrate (NO_3-N), Mehlich-3 P content and pH. Samples from summer 2008 were also analyzed for total N and total P. Samples from fall 2008 and summer 2009 were analyzed for K concentration.

Effects of N fertilizer and uptake by different hybrids on nutrient dynamics and pH of the soil water were analyzed using the PROC GLM procedure of SAS (SAS Inst., 2001). Effect of treatments in soil water was analyzed to determine week-by-week changes in nutrient concentration and pH. Effects of N fertilizer and uptake by different hybrids on nutrient content of the soils before and after harvest and nutrient content of each tissue of the hybrids were similarly analyzed using the PROC GLM procedure of SAS. Relationships between nutrients in the plant tissue were analyzed using the PROC REG procedure of SAS.

RESULTS

Nitrogen Composition of Hybrids

There was a significant difference ($P \leq 0.05$) between hybrids in grain N content (Table 6.1). The three newest hybrids that represent the decades from 1974 to 2005 had higher grain N content than the two older hybrids. Nitrogen fertilizer application rate also resulted in different levels of grain N ($P \leq 0.05$) in all three seasons (Fig. 6.1a). On average, nutrient content increased with increased amount of fertilizer.

Leaf N content was similar between all hybrids except P828 (the second-oldest hybrid), which had a lower N content than all other hybrids. Leaf N content was different at different N application rates ($P \leq 0.05$). Leaf N content increased with increased N rates.

The mid-era hybrid, P8585, contained the highest stem N content, and the oldest hybrid, RS610/P848, had the next highest stem N content. Stem N content also increased with increased N rates.

Similar to leaf N content, root N content across hybrids was not different except for P828 (the second-oldest hybrid) which had lowest N content of all the hybrids. However, unlike leaves, root N content was not different at different N rates.

Comparison of N content of tissues indicated that grain of all tested sorghum hybrids had the highest N (average of 16 mg N g^{-1}) than the leaves, stems, and roots. Nitrogen content of leaves was second highest with an average of 12 mg N g^{-1}. Stems and roots both contained 4 mg N g^{-1} (Table 6.1).

Phosphorus Composition of Hybrids

Similar to N content, grain had a higher P content (average of 4 mg P g^{-1}) than leaves, stems, and roots (Table 1). Phosphorus content of leaves was second highest with an average of 2 mg P g^{-1}. Stems and roots contained 1.6 and 0.8 mg P g^{-1}, respectively.

Hybrids released before 1974 had a lower ($P \leq 0.05$) grain P content than hybrids released after 1974. There was also a difference in grain P content in the three seasons. Nitrogen application rates did not affect grain P content.

Leaf P content was not different between hybrids but there was a difference in leaf P content due to both season and level of urea application. Leaf P content increased with increased urea application rates. Leaves contained more P in summer 2009 than in the other two seasons.

The mid-era hybrid (P8585, 1974-1984) had the highest stem P content and the second-oldest hybrid (P833, 1964-1974) had the lowest. There was a seasonal variation in the amount of P in the stem but there was no difference due to N rates.

Root P content of hybrids also was different. Root P content was lowest in the seecond-oldest hybrid and similar in all other hybrids. There was a seasonal variation in P content of hybrids in, but there was no difference due to N rates.

Potassium Composition of Hybrids

Unlike both N and P, grain contained the lowest K content of all the plant tissues (Table 6.1). Stem had the highest K content (about 36 mg K g^{-1}. Leaves, roots, and grain contained about 19, 8, and 4 mg K g^{-1}, respectively.

The newest hybrid (P85G46, 1994-2005) had the highest grain K content, and the second-oldest hybrid (P833, 1964-1974) had the lowest. All other hybrids had a similar grain K content. Nitrogen application rate was not significant, but there was significant seasonal variation in grain K content.

Leaf K content increased with hybrid advancement. There was a significant interaction between N rate and season for leaf K content (Fig. 1b). In the first and second season (summer and fall 2008) leaf K content was highest in the lowest level of urea application; the scenario reversed summer 2009.

The second-oldest hybrid (P833) had the lowest stem K content followed by the mid-era hybrid (P8585). The other hybrids (the oldest and the two newest hybrids) had the highest but similar K content. Root K content was not different between hybrids, but there was a significant interaction between season and urea application rate for root K content (Table 6.1).

In general, N-P-K content of grain and K content of leaves increased with hybrid advancement. There was also a significant linear relationship between N and P content of the hybrids (Fig. 6.2). The strongest N and P relation was found in grain ($R^2 = 0.92$) followed by leaves ($R^2 = 0.74$).

Total Nutrient Content

In total, sorghum hybrids contained about 680 to 990 mg N plant^{-1} (Table 6.2). About 60% of the N was allocated to grain, 19% to leaves, 11% to stems, and 10% to roots, and there was some variation between hybrids (Table 6.2). The two newest hybrids contained the highest total N mainly because of their greater root and leaf production (based on our previous study), and higher N composition per gram of grain.

Sorghum hybrids contained a total of approximately 170 to 250 mg P plant^{-1}. Similar to nitrogen, about 60% of the total P was allocated to grain. Leaves, stems, and roots contained about 13, 17, and 10%, respectively, of the P extracted. The newest hybrid had the highest P content, mainly because of high P concentrations and better root production compared with older hybrids.

Sorghum hybrids extracted about 930 to1800 mg K g plant^{-1}. Unlike N and P, 60% of the total K was in the stems. Grain, leaves, and roots contained the remaining 7, 18, and 13%, respectively, of the total K. Again, the newest hybrids had the highest K content because of increased K composition in grain and leaves and increased leaf and root production with hybrid advancement.

Nutrient Dynamics of Soil Water in the Growing Season

There was a difference in ammonium concentration of due to N fertilizer application rates at different weeks after planting (WAP) (Table 6.3). In the first WAP ammonium concentration in the soil water was highest for the highest N application rate (Fig. 6.3a). In the second WAP, the ammonium concentration dropped to almost zero in all pots and continued at this concentration until the end of the season. Neither hybrids nor interaction of hybrid and N level affected ammonia concentration in the soil water.

The amount of nitrate in the soil water was also different at different N application rates and different WAP (Table 6.3). In the first WAP, nitrate levels were about 0.3 ml l^{-1} in the control and about 0.65 ml l^{-1} in the 0.6 and 1.2 g pot^{-1} N application levels (Fig. 6.3b). In the second WAP, nitrate levels increased to about 0.45, 0.90 and 1.25 ml l^{-1} in the 0, 0.6 and 1.2 g pot^{-1} N application levels, respectively. Beginning in the third WAP, nitrate levels dropped approximately 0.1 ml NO_3 l^{-1} every week in all urea application levels, resulting in nitrate level of zero at 8, 11, and 16 WAP in pots with 0, 0.6, and 1.2 g pot^{-1} g N pot^{-1} application rates, respectively. There were no hybrid effects on nitrate levels in the soil water, and there was no significant hybrid by N interaction.

Phosphorus concentration in the soil solution fluctuated over time, and there was a difference due to N application rates (Table 6.3). The P concentration decreased at all N application rates in the first 6 WAP (Fig. 6.3d). In the seventh WAP, P concentration increased back to the original concentration for the control and the highest N application and it increased even higher than the original amount for the 1.2 g pot^{-1} N application rate. From the eighth WAP to the end of the season, P concentration remained almost constant and at about same concentration as the control and highest urea application levels at the seventh WAP except for a drop at the 12th and 16th WAP. There were no hybrid effects on P levels in the soil water, and there was no significant hybrid by N interaction.

Potassium concentration in the soil water also changed over time (Table 6.3). In the first WAP, there was approximately 0.14, 0.16, and 0.20 ml K l^{-1} in the soil solution of pots with 0, 0.6, and 1.2 g pot^{-1} N application rates, respectively. From the first to third WAP, K levels in the soil solution increased to 0.19, 0.24, and 0.25 ml K l^{-1} in pots with 0, 0.6, and 1.2 g pot^{-1} N application rates, respectively (Fig. 6.3). The concentration dropped about 0.03 ml K l^{-1} every week until the 8th, 10th and 11th WAP to 50 ml K l^{-1} for the 0, 0.6, and 1.2 g pot^{-1} N application rates, respectively. Similar to N and P levels, there were no hybrid effects on K levels in the soil water, and there was no significant hybrid by N interaction.

Neither N fertilizer rate nor hybrid significantly affected pH. However, pH in the soil water increased as the season progressed. The soil-water pH increased from 6.5 at the first WAP to 7.8 at 16 WAP (Fig. 6.4).

Nutrient Content of Soil

Compared with the soil at planting, the soil at harvest had a higher pH, about 6 mg kg^{-1} $soil^{-1}$ less in ammonium content, and about 44 mg kg^{-1} $soil^{-1}$ less nitrate and total N content (Table 4). Similarly, soil K content at harvest was 90 mg kg^{-1} $soil^{-1}$ less than that at planting. Mehlich and total P, surprisingly, increased from planting to harvest by about 57 and 36 mg kg^{-1} $soil^{-1}$, respectively.

At harvest, there was no difference between hybrids in ammonium, nitrate, P, K and pH of soils, but there was a difference between hybrids in total nitrogen. Except for P and pH, there were also no differences in measured nutrients due to different N application rates. The amount of P (both Mehlich-3 and total P) was lowest for the highest N application, and pH was higher for the two higher N application rates than for the control.

DISCUSSION

The main focus of the present study was to investigate nutrient use and allocation patterns with sorghum hybrid advancement. Results indicated an increase in grain N, P, and K concentration with hybrid advancement (Table 6.1). The total amount of N, P, and K extracted by hybrids also increased from the oldest to newest hybrids (Table 2). There is little information available on nutrient removal with sorghum hybrid advancement. However, Pal et al. (1982) reported that the newly introduced dwarf exotic hybrids (for India) had a higher nutrient content than the local tall varieties which were relatively old. It was also reported that development and release of new hybrids led to a relatively high yield increase in N-limiting areas, suggesting that improved hybrids have a better mechanism to extract nutrients (Doggett et al., 1970; Rao, 1982). After comparing several sorghum genotypes, Nakamura et al. (2002) indicated that N absorption was regulated by root activities and was higher in hybrids than in local varieties in low-N conditions. On the basis of previous result in our study (data not presented here), the main reason for higher nutrient uptake by improved hybrids in the present study was assumed to be due to better root and leaf biomass in the newer hybrids. Nakamura et al. (2002) reported a similar observation. Other reports also indicated differences between hybrids in nutrient uptake and the importance of root characteristics for increased nutrient use (Jacques et al., 1975; Maranville et al., 2002; Yan et al., 1995).

A few reports present data on nutrient uptake with advancement of genotypes of other cereal crops. Many of these reports agree with results presented in the present herein that newer hybrids have increased nutrient uptake. For example, wheat breeders reported that total nitrogen uptake increase with wheat genetic improvement (Austin et al., 1980; Calderini, 1995; Fisher, 1981; Fisher and Wall, 1976). However, there are also reports of no relation between nutrient uptake and genetic improvment (Slafer et al., 1990) and a negative relationship between genetic improvement in wheat and nutrient concentration in wheat grains (Calderini et al., 1995).

Our results also indicated that of all plant parts studied, sorghum grain contains the largest portion of N and P but lowest K concentration. Stem had the highest K concentration. We also found an increase in leaf K concentration with hybrid advancement (Table 1). These results agree with previous research reports (Vanderlip, 1993; Pal et al., 1982) that indicated a similar large portion of N and P in grain and K in the vegetative part of grain sorghum. The important role of K in drought tolerance was reported previously (Abu Assar et al., 2002; Bangar et al., 2004). Therefore, the increase in leaf K concentration and the increase in total K with hybrid advancement confirms that new hybrids tolerate drought better than older hybrids.

There was positive linear relationship between N and P uptake of sorghum hybrids (Fig 6.2). The strength of the relationship varied among plant tissues. The N and

P concentration had a stronger relationship in leaves and grain than in stems and roots. Jones (1983) previously reported a positive relationship in N and P concentrations in maize.

Soil water nutrient concentrations differed from planting through harvest. The sharp decrease in ammonium levels in soil water after 2 WAP was perhaps due to nitrification (conversion into nitrate). To sustain plant growth, the soil was subjected to subsequent watering and had good aeration, which would have facilitated nitrification in the soil. The nitrification process also explains the initial increase in nitrate concentration, whereas the initial increase in K concentration was perhaps due to dissolution from soil during watering. The decrease in both the nitrate and K concentration (2 and 3 WAP) can be explained by uptake by sorghum hybrids. Unlike N and K, P has a different nature in the soil. The fluctuation of P levels might be due to an initial P adsorption into soil from soil solution and dissolved applied fertilizer, dissolution due to complex formation with other nutrients, or plant uptake (wk 1 to 6, 12 and 16) and consequent desorption from soil to maintain equilibrium (wk 7 to11 and 13 to 15). The increase in pH levels was perhaps due to a decrease in ammonia and nitrate levels.

Similarly the soil solid nutrient content at planting was different from that at harvest (Table 6.4). Obviously, the decrease in N and K content of the soil was due to uptake by plants and losses through nitrification, and from plants at flowering. Harper et al. (1987) indicated same ways of nitrogen loss from soil in addition to plant uptake. The increase in P was due to initial application of DAP fertilizer, which was above the uptake by the hybrids.

Unlike the differences in nutrient uptake, there were no differences in the soil water and soil nutrient concentrations of ammonium, nitrate, P, and K in different WAP and at harvest due to hybrid treatments. This lack in differences might be due to a continuous diffusion or dissolution of nutrients from a pool of these nutrients (organic and inorganic) to soil water to maintain equilibrium or possible concentration. Maintaining equilibrium or a certain concentration in soil water usually comes with substituting the amount removed, as long as there are enough nutrients and the water is not saturated. Therefore, monitoring the soil water might not reflect differences unless there is a shortage in supply or the difference in uptake is too big of a difference to be equally compensated. Hybrids in this experiment were from the same species, and even if they differed in uptake the differences perhaps were not big enough to be reflected in the soil water. A similar explanation can justify the lack of difference between hybrids in soil nutrients, ammonium, nitrate, Mehlich-3 P, and K. The effect of differential uptake of hybrids, however, was reflected in total N content of the soil.

From these results we concluded that sorghum hybrid advancement was coupled with increased use of nutrients. Hybrids from different decades also allocated nutrients differently in different tissues. Newer hybrids can extract more primary nutrients than older hybrids perhaps because of increased root biomass that enable greater use of available resources.

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Table 6.1. N, P, K content of grain, leaves, stems, and roots of sorghum hybrids treated with different urea application rates.

Hybrid	Grain			Leaf			Stem			Root		
	N	P	K	N	P	K	N	P	K	N	P	K
	mg g⁻¹ of plant part											
RS610/P848	12.8c†	3.5b	3.5bc	12.4a	2.2	18.1c	4.2b	1.5b	36.0a	3.6ba	0.9a	9.0
P828/P833	14.1bc	3.5b	3.3c	10.2b	1.9	18.9c	3.2c	1.1c	32.4c	3.3b	0.6b	8.0
P8585	18.2a	4.3a	3.6abc	12.0a	2.3	18.4c	5.1a	2.1a	33.4bc	4.1a	0.9a	8.7
P5358	16.3ba	4.1a	3.7ba	11.4ba	2.0	20.1b	3.8bc	1.6b	37.2a	3.6ba	0.8ba	8.7
P85G46	16.6a	4.0a	3.8a	11.7ba	2.3	21.9a	3.5c	1.6b	38.9a	3.4ba	0.8ba	7.5
Nitrogen	N	P	K	N	P	K	N	P	K	N	P	K
g N pot^{-1}	**mg g^{-1} of plant part**											
0	3.0	3.6	3.7	7.1c	1.4c	20.4	2.6c	1.2	34.1	3.4	0.8	8.5
0.6	6.8	4.1	3.3	11.9b	2.1b	19.1	3.9b	1.6	34.6	3.3	0.9	7.6
1.2	7.4	4.0	3.6	15.7a	2.8a	18.9	5.3a	1.9	37.7	4.0	0.8	8.8
Season (S)	NS	***	***	***	***	***	***	**	***	***	***	***
Nitrogen (N)	***	NS	NS	**	**	NS	***	NS	NS	NS	NS	NS
S*N	***	NS	NS	NS	NS	***	NS	NS	***	NS	NS	**
Hybrid (H)	***	***	**	*	NS	**	***	***	**	**	**	NS
H *N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

† Means in the same column followed by the same letter are not significantly different (*P≤0.05*)

Table 6.2. Total N, P, and K content of grain, leaf, stem, and root of sorghum hybrids

Hybrid	Grain	Leaf	Stem	Root	Total by hybrid
			Total N		
	………………………….g plant^{-1}…………………….				
RS610/P848	0.41c†	0.15b	0.09	0.06c	0.71
P828/P833	0.48b	0.15b	0.10	0.07bc	0.80
P8585	0.41c	0.12c	0.08	0.08bc	0.68
P5358	0.50ba	0.14b	0.10	0.09b	0.83
P85G46	0.57a	0.19a	0.09	0.13a	0.99
Average N by part	**0.47**	**0.15**	**0.09**	**0.09**	**0.80**
			Total P		
RS610/P848	0.11bc	0.03b	0.03b	0.02b	0.19
P828/P833	0.11b	0.03b	0.03b	0.01b	0.19
P8585	0.10c	0.02b	0.03b	0.02b	0.17
P5358	0.13ba	0.03b	0.04a	0.02b	0.21
P85G46	0.14a	0.04a	0.04a	0.03a	0.25
Average P by part	**0.12**	**0.03**	**0.04**	**0.02**	**0.20**
			Total K		
RS610/P848	0.11b	0.22b	0.81b	0.16c	1.30
P828/P833	0.11b	0.28a	0.99a	0.17c	1.55
P8585	0.08c	0.18c	0.51c	0.16c	0.94
P5358	0.11b	0.25a	0.94a	0.22b	1.53
P85G46	0.13a	0.36a	1.02a	0.29a	1.80
Average by parts	**0.11**	**0.26**	**0.86**	**0.20**	**1.42**

† Means in the same column followed by the same letter are not significantly different (*$P \leq 0.05$*)

Table 6.3. Effect of urea fertilizer application and hybrid on pH and primary nutrient dynamics of soil water from planting to harvest

Factors	NH4-N	NO3-N	P	K	pH
			ml l^{-1}		
Nitrogen (N)	**	***	*	*	NS
Weeks (W)	***	***	***	***	***
N*W	***	***	NS	NS	NS
Hybrids	NS	NS	NS	NS	NS
H*W	NS	NS	NS	NS	NS
H*N	NS	NS	NS	NS	NS

*, **, *** means significant at 0.05, 0.01, and 0.001 probability level, respectively
† ns = non significant

Table 6.4. Average nutrient content and pH of the experimental soil before planting and after harvest for different hybrids treated with different urea application levels in three seasons.

Hybrid	Nutrient content after harvest						
	pH	K	NH4-N	NO3-N	Total N	Mehlich-3 P	Total P
	------------------------------mg kg^{-1} soil------------------------------						
RS610/P848	7.73	236.8	3.20	1.55	414.9a	112.1	323.8
P828/P833	7.74	245.1	2.50	1.42	412.2a	117.5	323.5
P8585	7.73	247.8	2.87	3.22	398.2ab	120.6	318.2
P5358	7.72	232.7	2.69	2.04	376.6b	114.9	313.7
P85G46	7.69	237.5	2.85	1.48	391.8ab	118.4	308.7
Nitrogen	pH	K	NH4-N	NO3-N	Total N	Mehlich-3 P	Total P
g N pot^{-1}	------------------------------mg kg^{-1} soil------------------------------						
0	7.66b†	247.7	2.68	1.51	409.2	131.7a	337.8a
0.6	7.73a	234.2	2.71	1.50		127.0a	
1.2	7.77a	247.7	2.98	2.66	415.5	102.1b	298.5b
Season (S)	***	***	***	NS	NE	***	NE
Nitrogen (N)	***	NS	NS	NS	NS	***	***
S*N	NS	NS	NS	NS	NE	NS	NE
Hybrid (H)	NS	NS	NS	NS	*	NS	NS
H*N	NS	NS	NS	NS	NS	NS	NS
Comparison of soil nutrient and pH before planting and after harvest							
	pH	K	NH4-N	NO3-N	Total N	Mehlich-3 P	Total P
Average at planting	7.3b	331.3a	8.4a	46.5a	443.5a	57.1b	271.7b
Average after harvest	7.7a	240.0b	2.8b	1.9b	398.7b	116.7a	317.6a

† Means in the same column followed by the same letter are not significantly different (*P≤0.05)*

† NS = non significant

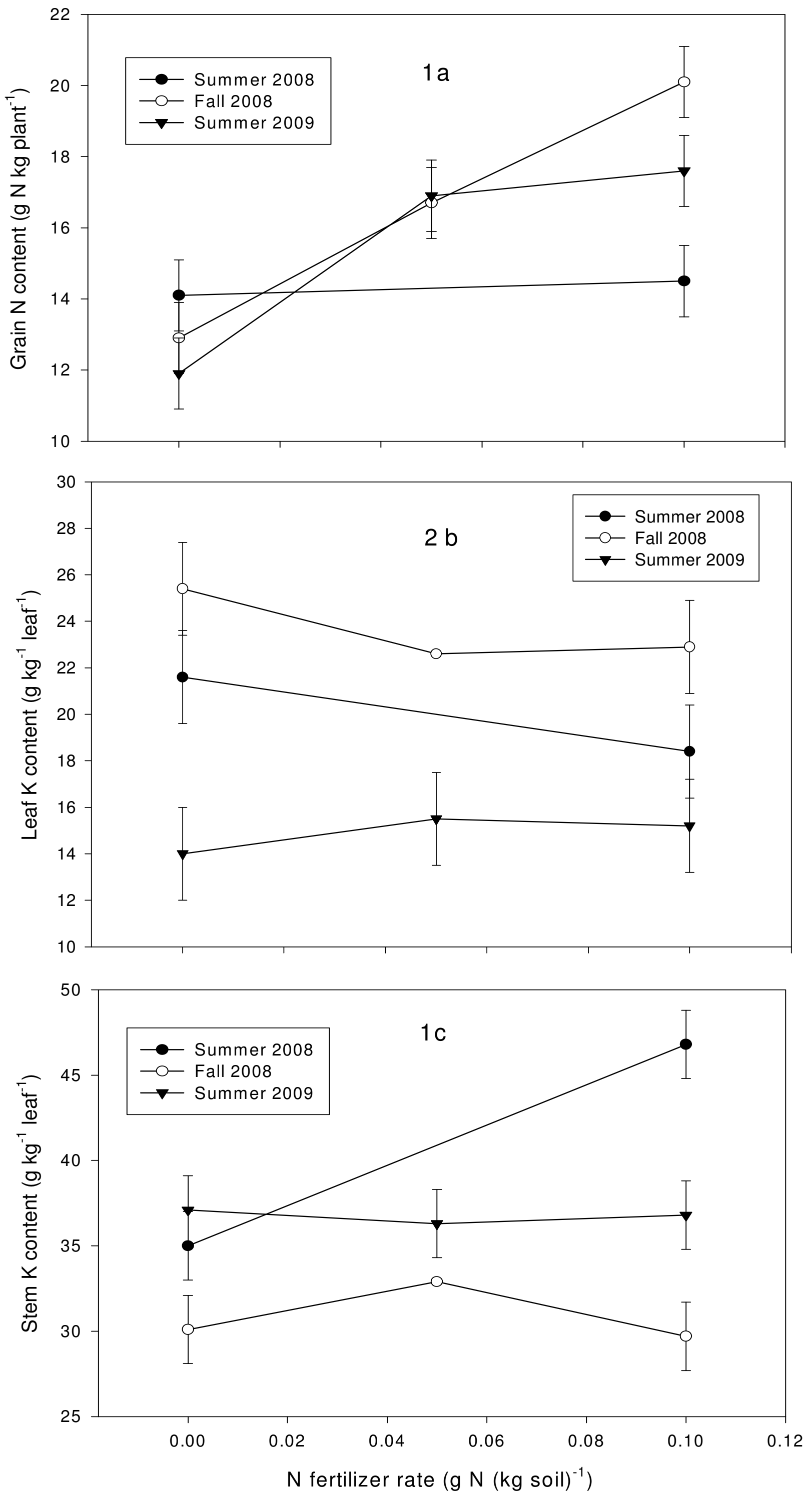

Figure 6.1 Grain N content and leaf and stem K content of hybrids treated with different urea application levels in different seasons.

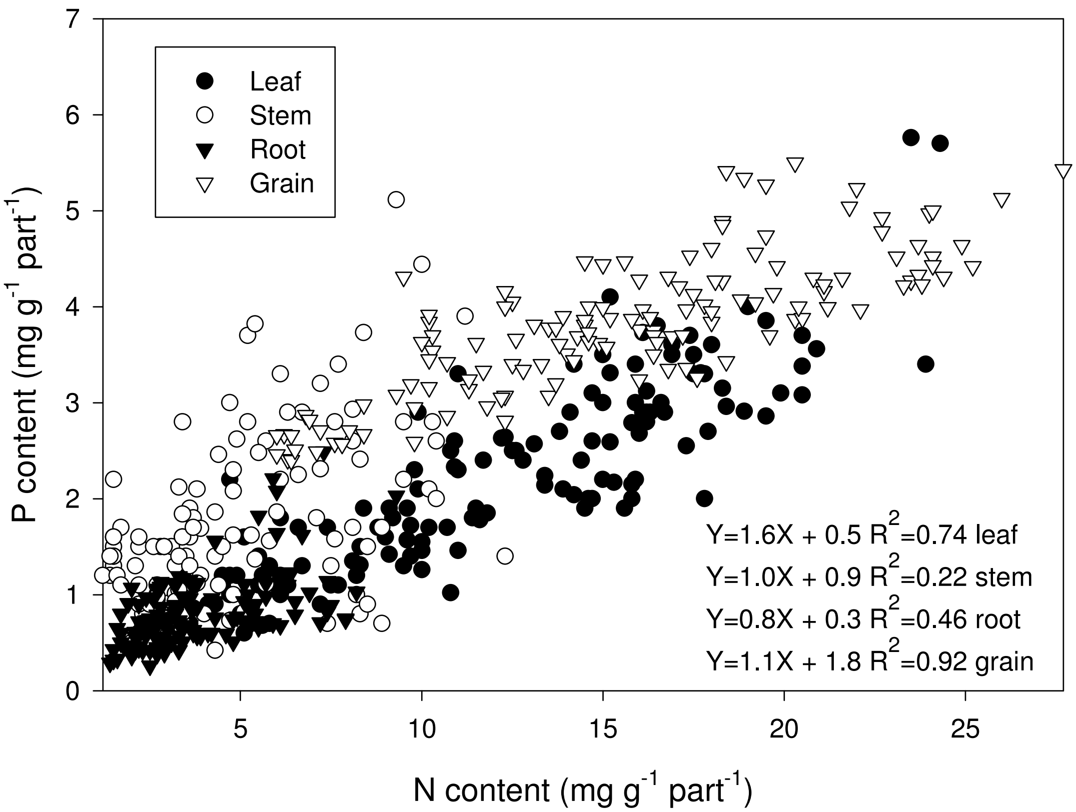

Figure 6.2 Relationship between P and N content of leaves, stems, roots, and grain of sorghum hybrids.

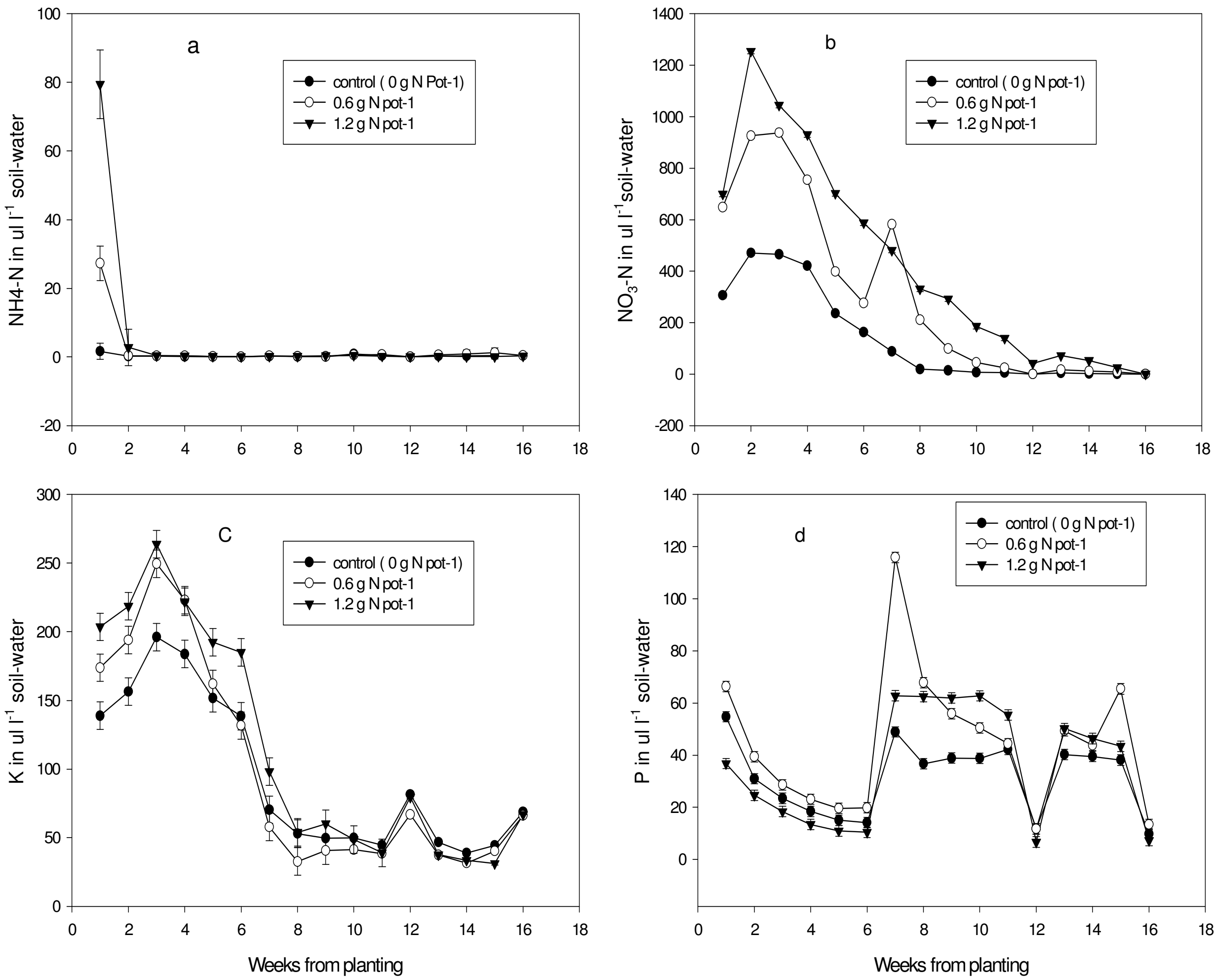

Figure 6.3 Dynamics of nutrients in soil water at different urea application rates and in different weeks after planting.

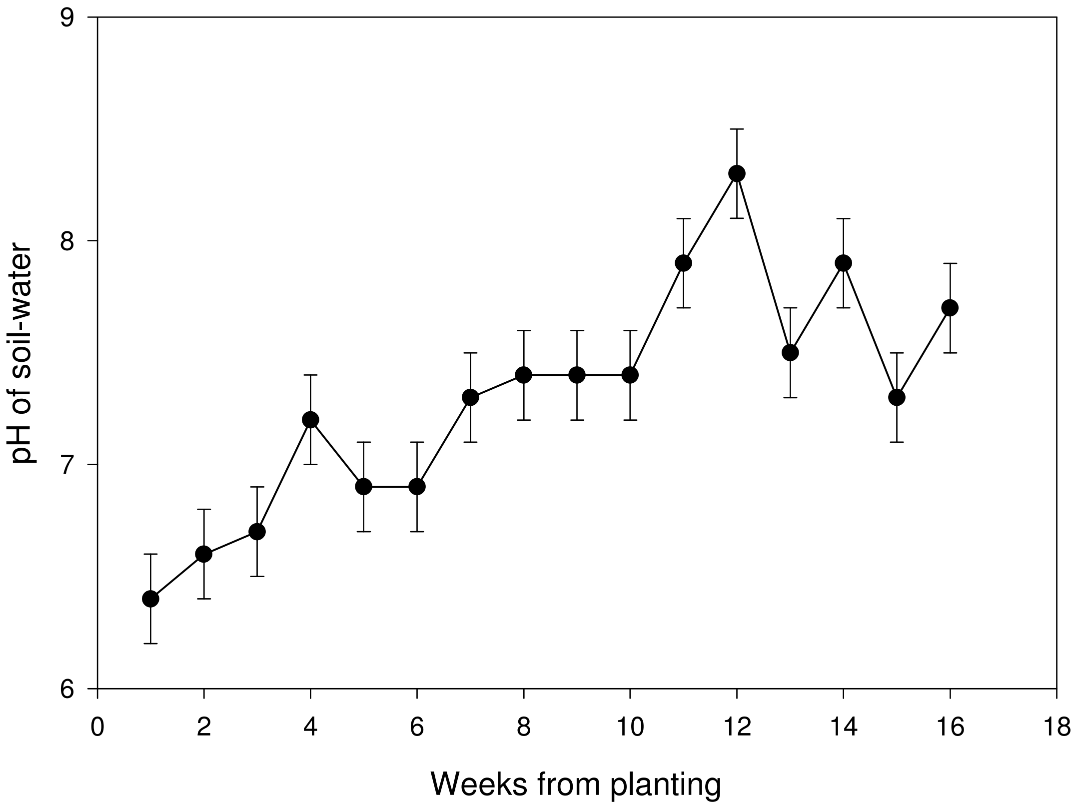

Figure 6. 4 pH of soil water at different weeks after planting.

Chapter VII

Comparison of New and Old Grain Sorghum Hybrids for Response to Planting Density

ABSTRACT

Change in planting density during the hybrid-era was evidenced for sorghum and it was concurrent with advancement of hybrids. This implies that old hybrids were historically planted in relatively lower densities compared with newer hybrids. Whether this difference in management for the two groups of hybrids happened randomly or it is based on a studied differential responses for the two groups is unknown. The objective of this research was to investigate response of old and new hybrids to different planting densities. A field study was conducted for two years, 2008 and 2009, at Manhattan, and Bellville, Kansas. Treatments were five Pioneer hybrids, each representing a decade from the past fifty years, planted at three densities. Results confirmed the increase in grain yield with hybrid advancement. At Manhattan, a significant decrease in seed weight with advancement of hybrids was observed. However, there was no effect on grain yield and number of heads at harvest due to different planting densities or the interaction of hybrids and densities. From these results we concluded that there was no change in grain sorghum response to different densities with hybrid advancement.

A significant change in planting density (distance between plants and rows) was reported for sorghum in the hybrid-era, beginning in 1957 (Assefa and Staggenborg, 2010). The change in planting density was concurrent with advancement of hybrids, i.e., the old hybrids were planted in relatively lower densities than the newer hybrids. However, whether this management difference is based on differential tolerance to density by the hybrids or just random practice is unknown.

An increase in tolerance to high planting density is an indicator for increased stress tolerance. Research indicated that increased planting density was one of the major factors that contributed to yield gain over years in corn (Tollennar, et al., 1991); and in soybeans (Cober et al., 2005; Specht et al., 1999). On the other hand, De Bruin and Pedersen (2009) argued that there was no change in soybean response to planting density with release periods.

A response variation for different densities among sorghum hybrids of different maturity groups was reported earlier (Blum, 1970; Wade and Douglus, 1990). Variable response for different densities among similar maturity hybrids was also evidenced (Wade et al., 1993). However, information on responses among old and new sorghum hybrids for different density was scarce.

The objective of this research was to investigate the response of old and new hybrids for different planting densities. We hypothesized that the new hybrids might have a better tolerance for high density planting than older hybrids. The background for our hypothesis was the fact that there was an increased drought tolerance due to increased in root biomass with hybrid release year, which perhaps might favor new hybrids in a competition for nutrient and water that would come with high density. To meet our objectives and proof our hypothesis, a field study was conducted in two sites on five hybrids planted in three densities.

MATERIAL AND METHODS

A field study was conducted for two years, in summer 2008 and 2009, at Manhattan (Ashland experimental station) and one year, in summer 2009 at Bellville (North Central Kansas Exp. Fld.). Treatments were five pioneer hybrids, each representing a decade from the past fifty years, planted in three densities, 15, 7, and 4 plants m^{-2}. The design of the experiment was split plot arrangement of a completely randomized design where densities were main plots and hybrids were the subplot.

At Manhattan, planting was conducted on May 6, 2008, and on April 26, 2009. Pre-emergence herbicides were applied two days before planting. The soil nutrient condition at planting were given in Table 7.1. Nitrogen fertilizer was applied in rate of 140 kg N ha^{-1}. Plants were sowed in the highest density and thinned to the required densities at approximately two leaf stage. In 2008, Pioneer hybrids 'RS610', 'P833', 'P8585', 'P8358', and 'P85G46' were planted. In 2009, 'P848' substitutes 'RS610' due to seed unavailability. Harvesting was possible in mid October, for 2008, and at the last week of September in 2009.

At Bellville planting was conducted on June 19, 2009. Planting was delayed due to wet weather conditions. Pre-emergence herbicides were applied immediately after sowing. Liquid nitrogen fertilizer was also applied 13 July, 2009, at rate of 112 kg N ha^{-1}. Similar to Manhattan, plants were sowed at the highest density and thinned to the required densities at approximately two leaf stage. Due to lack of seed, only four hybrids were tested at Belleville, i.e. P848, P833, P8358, and P85G46. Harvesting was conducted in second week of November.

Both 2008 and 2009 temperature and rainfall were favorable for rainfed sorghum at Manhattan (Table 7.2). Unlike the experiment in Manhattan, weather conditions in Bellville were not favorable. A very dry winter and spring; cooler and wetter than normal summer affected plant growth and yield.

At both sites, harvest was conducted manually. Number of harvested panicle were counted and cut from the plant at base of the panicle. Panicles then subject to dry in dryer at about 90^{o}C for a week. Grain yield was measured after threshing the seeds from the panicle. Samples of grain were taken for measuring moisture, test weights, and 200 seed weights.

The effect of treatments (hybrid and density) on yield, number of panicles m^{-2} at harvest, and seed weight were analyzed using PROC GLM procedure of SAS (SAS Inst., Cary, NC, 2001). Relationship between year of hybrid release with yield and seed weight was analyzed using PROC CORR procedure of SAS.

RESULTS AND DISCUSSION

Grain Yield

At Manhattan, there was a difference between hybrids in grain yield (Table 7.3). The lowest grain was from the oldest hybrid and the highest grain yield was from the newest hybrid. The other hybrid yields were in between, i.e. higher than the oldest but similar or lower than the newest. There was no yield differences ($P < 0.05$) due to differences in planting densities. The interaction between hybrids and density also was not significant. The correlation analysis indicated a yield increase with hybrid advancement, i.e., yield increased with year of release (Table 7.4).

Similarly, hybrids were different in grain yield at Bellville (Table 7.3). The newest hybrid had the highest grain yield, the rest of the hybrids, however, had similar yields. There was no significant effect of variable densities on grain yield. The interaction between hybrids and different densities was also not significant. Similar to results in Manhattan, the correlation analysis indicated that yield increased with hybrid advancement in Bellville (Table 7.4).

Number of heads at harvest

At Manhattan the number of heads at harvest was not different between hybrids and different densities. Overall, there were about 15 heads m^{-2} at harvest, which is equal to the maximum targeted population in this experiment (the highest density). This result supports that tillering contributes a significant portion to yield if sorghum is planted in low densities.

At Bellville, there was a difference in number of heads at harvest between hybrids. The second-oldest hybrid, P833, had a lower head number at harvest than the rest of the hybrids. However, there was no significant difference in head number at harvest between different densities. There were about 10 heads m^{-2} at harvest in Bellville, which was lower than the highest density but higher than the second-highest density in this experiment.

Seed Weight

Seed weight was different between hybrids in both Manhattan and Bellville. In both sites one of the newer hybrids, P8358, had the lowest seed weight. The oldest hybrid alone had the greatest seed weight followed by others at Manhattan. At Bellville, the greatest seed weight was from the oldest and newest hybrids. At Manhattan, seed weight was also different between different densities, i.e., seed weight of the lowest density was lower than the higher densities.

Correlation analysis showed that there was a significant negative relationship between hybrid advancement and seed weight at Manhattan (Table 7.4). There was a non-significant relationship between hybrid advancement and seed weight at Bellville, as well.

Results confirmed the increase in grain yield with hybrid advancement, which were evidenced by many authors (Assefa and Staggenborg, 2010; Duvick, 1999; Eghball and Power, 1995; Unger and Baumhardt, 1999). However, the lack of interaction between hybrid and density rejected our hypothesis that newest hybrids might have a better yield at higher densities than the old hybrids. A similar number of heads by all hybrids at harvest in Manhattan suggested that all hybrids compensated for lower densities by tillering in similar fashion. Larson and Vanderlip (1994) earlier suggested that grain sorghum compensates for lower densities by forming tillers. It is also reported that grain sorghum is able to compensate for densities below 12 plants m^{-2} (Conley et al., 2005; Gerik and Neely, 1987).

There was a variation in the average number of heads at harvest in two sites. In Manhattan, where growing conditions (mainly rainfall and temperature) in the growing season were favorable, number of heads m^{-2} and final yield were higher than at Bellville. Therefore, these results agree with the research report that suggested tillering is response to the level of resource available (Seetharama et al., 1984).

From the results we concluded that there was no change in grain sorghum response to different densities with hybrid advancement. Therefore, changes in other sorghum management practices, perhaps nitrogen fertilizer use and changes in hybrid resource use (water and nutrient) due to morphological changes in root and leaf density, are responsible for yield increase over years.

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Table 7.1. Soil analysis results for Manhattan (2008 & 2009) and Bellville (2009) experimental plots at planting

Sample Year	Depth	pH	Buffer pH	Mehlich 3 P	K	NH_4-N	NO_3-N	OM
	cm		SMP		Mg kg-1soil			%
				Manhattan				
2008	0-15	6.2	6.8	34	451	6.1	11.3	2.1
	15-30	6.2	6.9	13	311	5.2	8.1	1.9
2009		6.4	7.1	27	327	5.5	12.0	1.6
				Belleville				
2009	0-15	5.2	-	48	449	5.5	22.4	-

Table 7.2. Monthly (2008 & 2009) and Normal precipitations and Average (2008 & 2009) and normal Temperatures at Manhattan and Bellville, KS. Adapted from grain performance trial reports 2008 and 2009.

Month	Manhattan						Bellville			
	Precipitation (mm)			Average Temperature (^{o}F)			Precipitation (mm)		Average Temperature (^{o}F)	
	2008	2009	Normal	2008	2009	Normal	2009	Normal	2009	Normal
Nov. – Mar.	7.2	5.6	6.0	35	36	35	1.3	4.9	34	32
April	2.3	5.3	2.7	50	55	53	1.8	2.3	51	52
May	4.8	2.0	4.5	63	66	64	0.6	3.7	64	63
June	12.0	7.7	5.1	74	75	73	4.5	4.6	73	73
July	5.1	4.7	3.9	78	74	79	5.1	3.4	73	78
August	4.6	4.9	3.5	75	75	78	2.0	3.4	73	77
Sep.	5.4	1.5	3.8	67	62	70	1.9	3.5	65	68
Oct.	4.4	2.2	2.8	61	48	57	3.1	1.8	47	55
Totals	45.8	34.0	32.4	53	53	54	20.2	27.5	51	52

Table 7.3. Effect of treatments on grain yield, heads at harvest, and seed weight at Manhattan (two years combined) and Belleville

Hybrid	Manhattan			Belleville		
	Grain Yield	Number of Plant at Harvest	200 Seed Weight	Grain Yield	Number of plant at harvest	200 Seed weight
	Mg ha^{-1}	Heads m^{-2}	g	Mg ha^{-1}	Heads m^{-2}	g
RS610/P848	4.0c	13.1	7.4a	2.7b	11.0a	6.3a
P828/P833	5.0ab	14.0	6.4b	2.5b	08.9b	5.3b
P8585	4.8b	15.4	6.1b	-	-	-
P5358	5.3ab	15.1	5.5c	2.5b	11.0a	5.0c
P85G46	5.7a	15.2	6.4b	3.2a	12.0a	6.0a
Density (plants m^{-2})	Mg ha^{-1}	Heads m^{-2}	g	Mg ha^{-1}	Heads m^{-2}	g
15	4.9	15.0	6.1b	2.9	12	5.6
7	5.0	13.9	6.5a	2.7	10.1	5.7
4	5.0	14.8	6.4a	2.7	10.3	5.6
Replication (R)	NS	NS	NS	NS	NS	NS
Density (D)	NS	NS	*	NS	NS	NS
D*R	NS	NS	NS	NS	***	NS
Hybrid (H)	***	NS	***	***	**	***
H *D	NS	NS	NS	NS	NS	NS

Table 7.4. Correlation between hybrid release period with grain yield and seed weight at Manhattan and Belleville

	Manhattan		Bellville	
Correlation Analysis	Grain Yield	Seed Weight	Grain Yield	Seed Weight
Correlation coefficient release period of Hybrid	0.516	-0.605	0.373	-0.177
P>r	<0.01	<0.01	0.02	<0.31
Number of observations	84	43	35	35

GENERAL SUMMARY

The objectives of this study were to (1) determine the magnitude of yield change, in the hybrid-era, in irrigated and dryland sorghum production, (2) determine the contribution of agronomic and hybrid changes for yield in the hybrid-era, (3) investigate changes in sorghum morphology, physiology, and water use that contributed to yield increases, (4) investigate changes that accompanied yield increase with hybrid improvement, and (5) to understand the general sorghum water and nutrient use and existence of variation between hybrids.

The study found out that there was an increase in hybrid yield of nearly 50 kg ha^{-1} yr^{-1} in dryland sites over the 52 yrs analyzed. Irrigated grain sorghum yields, however, remained unchanged over the same period. Agronomic practices such as planting date, phosphorus fertilizer use, and planting density changed over these years but were not found to contribute to increased dryland sorghum yields. Hybrid advancement and increased nitrogen fertilizer application were responsible for changes in dryland yields.

In an effort to answer how hybrid advancement contributed to yield, the study found out that total water use changed from old to new hybrids. The new hybrids used the greatest total water in the well-watered treatments and also had greater root-to-total biomass ratio than the old hybrids. Leaf biomass was also greater for the newest hybrid. Moreover, there was a difference in the amount of total nutrients extracted by hybrids, and there were differences between hybrids in allocation of nutrients to different plant parts. Results indicated that new hybrids can extract more primary nutrients than old hybrids.

Therefore we concluded that the yield focus of sorghum hybrid development was effective in dryland sorghum production, likely because of intentional or inadvertent selection of hybrids with better drought tolerance. Hybrid development programs created hybrids with improved morphological characteristics that might have resulted in better resource use and ultimately to an increase in yield.