RESPONSES OF MAIZE (*Zea mays* L.) LANDRACES TO WATER STRESS COMPARED WITH COMMERCIAL HYBRIDS

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DECLARATION

I, Tafadzwanashe Mabhaudhi, certify that the material reported in this thesis represents my original work, except where acknowledged. I further declare that these results have not otherwise been submitted in any form for any degree or diploma to any university. This study was financially supported by the Water Research Commission (Project No. K5 /1771//4).

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I, Albert Thembinkosi Modi, supervised the above candidate in the conduct of his dissertation study.

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Prof. A.T. Modi

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DEDICATION

This work is dedicated to God Almighty who has blessed my life with all the people I call dear and cherish.

ABSTRACT

Local maize landraces have evolved over hundreds of years of natural and farmer selection under varying conditions. These landraces may have developed tolerance to abiotic stresses such as water deficits during this cycle of selection. However, despite its continued existence and importance, little is known on their agronomy and responses to water stress. If indeed landraces have developed tolerance to water stress, they may prove a key genetic resource for future crop improvement in light of increasing water scarcity. The primary objective of this study was to evaluate the responses of a local maize landrace to water stress at different stages of growth in comparison to two known commercial hybrids, SC701 and SR52.

Seed from a local maize landrace was multiplied and characterised according to kernel colour. Two distinct colours were selected for the purposes of this study, white (Land A) and dark red (Land B). In a holistic approach, the thesis consisted of four separate studies whose overall objective was to evaluate the responses of the maize landraces to water stress at different growth stages, up to and including yield and its components. These comprised three controlled environment studies (25℃; 60% RH) and a field trial. For the controlled environment, two water regimes were used, 25% field capacity (FC) (stress treatment) and 75% FC (non-stress).

The first study investigated the effect of water stress on early establishment performance. Seed quality was evaluated using the standard germination test

together with electrolyte leakage. Catalase activity and accumulation of proline were examined as seedling physiological response to water stress. The second study was conducted as a pot trial to investigate the effect of water stress on growth, photosynthesis and yield. Photosynthesis was measured as chlorophyll fluorescence (CF).

In addition, a field study over three planting dates was conducted at Ukulinga Research Farm in Pietermaritzburg, under dryland conditions, during the period from August 2008 to June 2009. The objective was to evaluate the effect of planting dates and changing soil water content on growth, yield and yield components. Three planting dates were used, representative of early (28 August 2008), optimum (21 October 2008) and late planting (9 January 2009).

Lastly, a study on hydro-priming was conducted, necessitated by observations made primarily in the first study. The study was carried out under controlled environment conditions. The objective was to evaluate whether hydropriming can improve germination, vigour and emergence under water stress. Seeds were soaked in water for 0 hours (Un-primed or control), 12 hours (P12) and 24 hours (P24).

Results from the first study showed that maize landraces were slower to germinate and emerge, and produced less vigorous seedlings compared to the hybrids. The study showed that hybrids were more superior under optimum (75% FC) conditions than under stress conditions (25% FC). Physiological showed that both hybrids and landraces expressed catalase under water stress, with landraces showing slightly

better expression compared to the hybrids. Proline accumulation was observed in both hybrids and landraces as a response to water stress, with hybrids being more sensitive to water stress.

In the pot trial, results showed that the vegetative stage of both hybrids and landraces was less sensitive to water stress than the reproductive stage. Results showed no differences between field capacities, with respect to emergence, mean emergence time, leaf number, CF, ear prolificacy and ear length. Photosynthesis, as measured by CF, was shown to be desiccation tolerant. Water stress had a negative effect on cob mass, lines per cob, grains per cob and total grain mass, and resulted in barrenness in the landraces. The hybrids had superior yield compared to the landraces.

Results for the field trials showed that planting date had highly significant effects on emergence, plant height, leaf number and days to tasseling (DTT). Landraces emerged better than hybrids in all plantings; highest emergence was in the early and late plantings. Optimum and late planting resulted in maximum plant height and leaf number, respectively, compared to early planting. Hybrids were superior, growing taller and with more leaves than landraces in all plantings. DTT decreased with successive plantings. Planting date had an effect on ear prolificacy (EP), kernels/ear (KNE) and 100 grain mass. Planting date had no effect on ear length and mass, kernel rows/cob, grain mass and yield. With the exception of EP, hybrids out-yielded the landraces in all three planting dates.

Hydro-priming landraces for 12 hours and 24 hours, respectively, improved germination velocity index, reduced mean germination time and improved emergence and mean emergence time of maize landraces under water stress. Performance of hybrid seeds remained superior to that of landraces even after seed treatment to improve germination and vigour.

Landraces were slower to germinate and emerge and produced less vigorous seedlings in controlled conditions only. Both hybrids and landraces expressed catalase activity and also accumulated proline in response to water stress, although hybrids were more sensitive to stress in the establishment phase. Results confirmed literature, showing that, for both hybrids and landraces, the vegetative stage is less sensitive to stress than the reproductive stage. Hybrids produced superior yields compared to landraces in both controlled environment and field conditions. However, the pattern of seedling establishment observed in the initial controlled environment study for hybrids and landraces was reversed in the field study. Lastly, hydro-priming is of some benefit to maize establishment.

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CHAPTER 1

LITERATURE REVIEW

1.0 Introduction

Of the many crops grown in South Africa (SA), maize (*Zea mays*, L) is one of the staple foods. Maize (*Zea mays,* L.) belongs to the family Poaceae (Gramineae) and the tribe Maydeae (Sikandar *et al*., 2007). In terms of global production, it is the third most important cereal, after wheat and rice, respectively. It is one of the staple food crops of the world and the staple cash crop of southern Africa (Burtt-Davy, 1914). About half of its global production is in developing countries, where maize flour (mealie-meal) is the staple food. It also has many diversified uses which include: starch products, corn oil, baby foods, popcorn, etc.

Maize is also referred to as corn or Indian corn in the United States and Great Britain and is one of the most widely distributed food plants today (Andrews, 1993). Although the exact origins of maize are still a point of academic debate, there seems to be general consensus that maize originated in Mexico, South America. The name *maize* is believed to come from the Arawak *mahiz.* Experts have established that modern maize came from *teosinte* (God's corn) or *Zea mays ssp. Mexicana* (Beadle, 1939).

In Sub-Saharan Africa, maize is the staple for an estimated 50% of the population and provides 50% of the calories. It is an important source of carbohydrate, protein,

iron, vitamin B, and minerals. In South Africa, in addition to the traditional uses, the government is also considering maize fuel: an alcohol based alternative fuel produced by fermenting and distilling the rich starch grains of the crop.

According to FAO statistics, maize yields currently average 1.5 t/ha in Africa. Most of the crop is grown under dryland conditions by small-scale farmers, mainly for subsistence purposes and as part of a multi-enterprise agricultural system. This system often lacks inputs such as fertilizers, improved seed, irrigation and labour. In most developing countries there are very little purchased inputs for the cropping system and it mainly depends on the natural resource base (Ofori & Kyei-Baffour, 2008).

Rainfall is the single most important natural resource input and limiting factor under this traditional system of cropping. Rainfall distribution in South Africa is uneven throughout the country (South African Weather Service, 2008). SA is a dry country with less than 500 mm mean annual rainfall recorded over about two-thirds of its area; compared to a world average of 836mm mean annual rainfall. Drought is a normal, recurrent feature of the South African climate and has in the past resulted in significant economic, environmental, and social impacts. Climate change is expected to have a severe impact on agriculture as it is expected that the frequency of drought will increase. This will have a negative effect on farming, especially on rural farmers, farming already on marginal lands (Hassan, 2006).

Historically, rainfall has been the single biggest cause of yield losses in agriculture (Duvick, 1997; Cassman, 1999). Poor rainfall has always resulted in many subsistence families going hungry in times of drought as their crops fail. This has led to researchers directing their efforts towards the development of drought-resistant or drought-tolerant cultivars. This has been the case since the 1930s when Africa's maize revolution started taking shape. Emphasis has been put on developing high yielding varieties that can withstand water stress.

However, noble as these efforts might be, they have resulted in indigenous and traditional crops receiving scant attention from researchers in Africa, including South Africa, with regards to improving agronomic practices and upgrading their genetic potential. There seems, however, to have recently emerged new interest amongst South Africans towards these crops. Local maize varieties (landraces) have often been shunned by researchers in favour of developing drought tolerant hybrids, although many farmers still grow them. This is evident from the apparent lack or inadequacy of information concerning responses of landraces to crop stresses, of which water is the most significant. Responses of landraces to drought stress and adaptability to the most varied of conditions, for which landraces are reputed, have been least studied.

This study aimed to study a local maize germplasm with the aim of comparing it to two popular cultivars, SR52 and SC701, with respect to water stress tolerance.

1.1 Maize as a Traditional Crop in Southern Africa

All maize varieties belong to a single species, *Zea mays*, but the number of varieties, adapted to the most varied environmental conditions, is numerous (Arnon, 1972). Most of the cultivated varieties belong to two maize groups, Horse-tooth and Flint maize. The Horse-tooth are those with the greatest yield potential whilst the Flint varieties are better adapted to adverse growing conditions.

Despite some earlier controversy, it now seems clear that the Portuguese first introduced maize into Africa during the 16th century (Miracle, 1966; McCann, 2005). Early Portuguese merchants introduced maize into Africa through their trade networks along the eastern and western coasts of Africa starting in the 16th century. The Dutch introduced maize along the southern African coast in 1658 (Miracle, 1966). The Afrikaans word for maize, "*mielie*" is a corruption of the Portuguese word *milho*, meaning grain (Burtt-Davy, 1914). Caribbean and Brazilian flints such as yellow-to-orange *Cateto* variety had hard endosperm, were early maturing, and had variegated bright coloured grains. These varieties formed the now local maize populations or landraces. Although maize may have its ancestry outside of Africa, it has been around for so long and has become indigenised as a result of hundreds of years of farmer and natural selection.

Zeven (1998) defined landraces as crop genetic resources that have evolved continuously under natural and farmer selection practices rather than in the collection of gene banks or plant breeding programs. Apart from being identified by its local names, landraces also possess other unique characteristics which distinguish them

from improved varieties. Historically, landraces were the progenitors of modern crop varieties. Landraces possess certain unique phenotypic, morphological and phenological characteristics as well as a reputation for adaptation to local climatic conditions and cultural practices, resistance and tolerance to disease and pests. As a result, landraces usually have yield stability and intermediate yield levels under a low input agricultural system (Zeven, 1998).

The term “hybrid” refers to a first generation progeny of a cross between two different strains of the same species. A hybrid may combine characteristics derived from the two parents and may be more desirable than either parent (Stoskopf, 1981). The SR52 hybrid was the first to be introduced in southern Africa and was released in 1960 and is still very popular amongst local farmers in KwaZulu-Natal. It was a long season variety (158 days) with yields of 7-12t/ha. Its release marked the start of the first African green revolution (Derek & Eicher, 1994).

However, the higher yield potential of hybrids is of value only if environmental conditions make it possible to exploit this advantage; when crops are grown under adverse growing conditions, hybrids may be inferior to well-adapted open-pollinated varieties (Stoskopf, 1981).

As a result of this, and partly due to the cost of hybrid seed, small-scale farmers in traditional farming systems of KwaZulu-Natal continue to use landraces which they have kept from generation to generation. Although these farmers are still planting

maize landraces to this day, there has been little or no research to characterize these landraces with respect to drought tolerance and adaptability to water stress.

1.2 Drought and Water Stress

Plant water stress, often caused by drought or a large variation in rainfall, can have major impacts on plant growth and development. The SA Weather Service defines drought on the basis of the degree of dryness in comparison to “normal” or average amounts of rainfall for a particular area or place and the duration of the dry period-meteorological drought. In crop production, there is physiological drought. This is when there is insufficient moisture in the soil to support plant growth and development. This can occur as a result of a meteorological drought, poor rainfall distribution during the duration of the growing season and poor cultural practices which effectively reduce soil water content resulting in the plant being water stressed.

Drought, through insufficient rainfall and poor distribution during growth, is one of the most important abiotic stresses affecting maize production (Ofori & Kyei-Baffour, 2008). It is the single most important source of variation in yield over time; highlighting our continuing vulnerability with regards to this natural phenomenon (South African Weather Service, Drought Monitoring Desk, 2008).

Although maize has its origins in a semi-arid climate, it is not a reliable crop for growing under dryland conditions with limited or erratic rainfall (Arnon, 1972). Maize is apparently more drought resistant in the early stages of growth than when fully

developed. This may explain why the practice of sowing maize early is desirable despite the danger of wilting during periods between light showers which precede the rainy season. The early sown maize has the advantage of a longer growing season than later-sown maize, though the latter is sown under more favourable conditions of moisture (Glover, 1959). Extreme water stress at different stages of crop development has been reported to reduce yield significantly (Dhillon *et al*., 1995). The response of the maize crop to climate depends on the physiological makeup of the variety/hybrid being grown. Yield differences are the result of genetic composition of the variety/hybrid, the environmental conditions under which the crop is grown and the infestation of plant pests.

1.3 Effect of Water Stress on Maize Growth

1.3.1 Crop Establishment

Traditionally, the first crop of maize is sown in late-Spring, before the onset of the rainy season when the soil is still too dry to support good germination and emergence. This often results in poor emergence and crop stand. Seeds sown in seedbeds with unfavourable soil moisture have been shown to have poor and unsynchronised emergence (Mwale *et al*., 2003). Water stress has been shown to decrease both percentage and rate of germination in numerous crops; *Senna occidentalis* seeds (Delachiave & Pinho, 2003), wheat (Radhouane, 2007; Rauf *et al*., 2007) and maize varieties (Mohammadkhani & Heidari, 2008). Poor germination and emergence, as a result of water stress, can have serious deleterious effects on crop

stands and ultimately yield. As such, the response of seeds to drought could prove an important indicator to plant stress tolerance in later growth stages.

The intimate relationship between seed quality and ability to germinate under unfavourable conditions and to establish maximum crop stand cannot be taken for granted. Seed quality confers a seedlot's ability to establish an optimum plant stand in both optimum and sub-optimum conditions. However, there is not much written in literature about the seed quality of maize landraces and its relation to drought. The huge variability that also exists within maize landraces may also explain the gap in literature.

1.3.2 Leaf Area Development

Leaf area is the measure of the photosynthetic system; it is the sum of all leaf laminae (Stoskopf, 1981). All aspects of agricultural production are intimately associated with the growth of leaves (Milthorpe, 1956) because photosynthesis is usually proportional to leaf area. However, green leaf area does not always equate with actively photosynthesizing leaf area (Valentinuz, 2004).

Water stress has been shown to reduce leaf area (Jun-Chen & Dai-Junying, 1996). Reduction of leaf area is a drought avoidance mechanism, which reduces plant water use rate and hence conserves water during periods of drought (Ludlow & Muchow, 1990; Jones, 1992). This reduction of leaf area is attributed to inhibition of individual leaf expansion and reduced total number of leaves per plant (Chartzoulakis *et al*.,

1993; Belaygue *et al*., 1996). Reduction of the number of leaves per plant under water deficits can be brought about by reduction of leaf appearance rate, branch formation in species that do branch (or tiller), leaf number per branch, plant height as well as accelerated leaf senescence (Carberry *et al*., 1993a, b; Belaygue *et al*., 1996; Marcelis *et al*., 1998; Gupta *et al*., 2001; Pic *et al*., 2002;). The extent of reduction of leaf appearance rate depends on the timing and duration of the stress period (Belaygue *et al*., 1996).

The reduction of individual leaf area involves inhibition of expansive growth of the leaf. Expansive growth results from cell division and enlargement, which involves extensibility of the cell wall under turgor pressure (Pugnaire *et al*., 1999). Under limited water supply, turgor pressure is reduced and growth becomes dependent upon the rate of water supply (Jones, 1992). Reduction in leaf area can thus be considered to be a plant's first line of defence against drought.

1.3.3 Root Development

Root development is an important factor determining the adaptability of a given plant to water stress conditions (Russell, 1959). Water stress enhances root growth and enhanced root growth is a plant's second line of defence to drought.

Water stress not only influences dry matter production, but dry matter partitioning as well (Jones, 1992). Studies indicated that relatively more dry matter is partitioned to the roots as compared to the shoot in plants facing drought (Wilson, 1988; Li *et al*.,

1994; Lehto & Grace, 1994; Wien, 1997; Arora & Mohan, 2001). Increase in root:shoot ratios under drought has been attributed to the fact that shoot growth is more sensitive to increasing soil water stress than root growth (Kramer & Boyer, 1995) as has been shown in cowpea (Sangakkara, 1998), French beans (Sangakkara *et al*., 1996a, b), soybean (Huch *et al*., 1986) and various C4 grasses (Fernandez *et al*., 2002). Generally, roots will grow until the demand for photosynthate from the shoot equals the supply.

1.3.4 Dry Matter Partitioning

By limiting leaf area development, water stress reduces radiation interception by plants. Consequently, less biomass is produced as has been reported in most crops (Singh, 1991; Jones, 1992; Sadras *et al*., 1993; Turc & Lecoeur, 1997; Nam *et al*., 1998; Delfine *et al*., 2000). In addition, the reduction in stomatal conductance caused by water deficits leads to reduced carbon assimilation and consequently low biomass production (Kumar *et al*., 1994; Delfine *et al*., 2000, 2001; Medrano *et al*., 2002). Furthermore, water stress can negatively affect the photosynthetic system of the plant. An example is through inactivation of enzymes involved in photosynthesis (Chaves *et al*., 2002; Lawlor, 2002; Medrano *et al*., 2002). This inactivation can be due to an increase in leaf temperature beyond a certain threshold, for instance 30℃ in maize (Crafts-Brandner & Salvucci, 2002), resulting from reduced transpirational cooling that accompanies reduction of transpiration under water stress (Jones, 1992).

1.3.5 Growth, Development and Yield

Stem height is significantly affected by water stress (Khan *et al*., 2001). Plant height has been shown to decrease due to water stress (Hernandez, 1980; Porro & Cassel, 1986). Khan *et al*. (2001) found that water stress decreased the grain yield of maize through decreasing stem height and leaf area.

Grain yield of maize is most susceptible to water stress during flowering, tasseling and silking (Shaw, 1977). Water stress slows ear growth, and consequently silk emergence, more than tassel growth or anthesis, resulting in a widening interval between anthesis and silking (Bolanos & Edmeades, 1996). In research carried out in the United States of America (USA), the greatest yield reduction was associated with stresses that were most intensive during the 25 day period after flowering (Campos *et al.*, 2004).

1.4 Effect of Water Stress on Maize Physiology

1.4.1 Chlorophyll Fluorescence (CF)

According to Lemon (1966), photosynthesis is the basis of all crop yield. Luna *et al.* (2004), working on wheat, observed severe inhibition of photosynthesis when soil water content decreased to 30%. Chlorophyll fluorescence (CF) analysis has become one of the most powerful and widely used techniques available to plant physiologists. CF can give an insight into the ability of a plant to tolerate water stresses and the

extent to which those stresses have negatively impacted on the photosynthetic apparatus (Maxwell & Johnson, 2000).

CF is based on the Kautsky (1960) effect. In green tissue, photosynthetically active radiation (PAR) is absorbed by chlorophyll and accessory pigments of the protein-chlorophyll a/b apparatus, and it migrates to the reaction centres of photosystem I and II, where the quantum photosynthetic process takes place (Horton *et al*., 1996). Based on this, measurement of CF is considered an important technique in eco-physiological studies of plants (Goedheer, 1972; Govindjee *et al*., 1981; Havaux & Lannoye, 1983; Krause & Weis, 1991). Use of CF parameters, such as F_o (initial), F_m (maximum), F_v (variable= F_m-F_o), F_v/F_m to evaluate intact leaves, make it possible to estimate photosynthetic efficiency of the leaf, under various conditions (Durães *et al*., 2001). The F_v/F_m ratio (the measurement of quantum yield potential of photosynthesis, or maximal photochemical efficiency of PSII) has been shown to be a reliable stress indicator (Krause & Weis, 1991; Schreiber *et al*., 1994).

Severe levels of drought may irreversibly damage the photosynthetic apparatus (Zulini *et al*., 2007). While several physiological traits have been associated with stress tolerance in maize and other crops (Bolaños & Edmeades, 1993; Cárcova *et al*., 2000; Mu-Qing *et al*., 2000; Durães *et al*., 2000, 2001), measurement of CF is considered important (Goedheer, 1972; Krause & Weis, 1991).

1.4.2 Protein Synthesis and Accumulation

Changes in protein expression, accumulation and synthesis have been observed in plants exposed to drought (Chen & Tabaeizadeh, 1992; Cheng *et al*., 1993). Girousse *et al.* (1996) observed that during prolonged periods of drought, the decrease in water availability led to changes in the concentrations of many metabolites followed by disturbances in amino acid metabolism. Riccardi *et al*. (1998) observed quantitative and qualitative changes to proteins in leaves of two maize genotypes during drought stress and concluded that protein quantity was differently modified by stress, according to genotype.

In maize, drought stress has been reported to increase the expression of some 50 proteins, decrease expression of 23 and to induce the synthesis of 10 other proteins (Riccardi *et al*., 1998). Proteins synthesized in response to drought are called dehydrins (dehydration induced) and belong to the group II late embryogenesis abundant (LEA) proteins (Close & Chandler, 1990), which range from 9-200kDa (Close, 1996). Evidence is increasing in favour of a relationship between the accumulation of drought-induced proteins and physiological adaptations to drought (Bray, 1993; Han & Kermode, 1996; Riccardi *et al*., 1998).

1.4.3 Antioxidant Response

Photosynthesis is particularly sensitive to water deficit because stomata close to conserve water as available soil water declines. Stomatal closure deprives leaves of carbon dioxide and photosynthetic carbon assimilation is decreased in favour of

photorespiratory oxygen uptake (Luna *et al*., 2004). As a result of stomatal closure and the subsequent photorespiration, an increase in reactive oxygen species (ROS) occurs, also known as free radicals. These, in particular hydrogen peroxide (H_2O_2), can cause oxidative damage to the plant. H_2O_2 is also generated as a secondary messenger in abscisic acid (ABA)-mediated stomatal closure (Pei *et al.*, 2000). In photorespiration, H_2O_2 is produced at very high rates by the glycollate oxidase reaction in the peroxisomes (Noctor *et al.*, 2002).

However, plants have various physiological strategies to respond to diverse environmental stresses such as drought (Pastori & Foyer, 2002) and minimize oxidative damage. Studies have shown that there exists a relationship between antioxidant activity and the ability of plants to tolerate water stress in wheat (Luna *et al*., 2004) and maize (Ti-da *et al*., 2006; Mohammadkhani & Heidari, 2007). H_2O_2 is eliminated by catalases (CAT) (Chen & Asada, 1989; Scandalios *et al.*, 1997). Catalase is the principle H_2O_2 scavenging enzyme in plants and is located in peroxisomes/glyoxisomes (Asada, 1999) and is an example of oxygen-scavenging systems consisting of several other antioxidants, such as ascorbate peroxidase (APX) and guaiacol peroxidase (GPX) (Noctor & Foyer, 1998).

1.4.4 Proline Accumulation

Proline accumulation in water stressed plant tissue was first observed by Kemble and MacPherson (1954). Since then, accumulation of proline has been reported as a widespread plant response to environmental stresses, including water stress (Yancey

et al., 1982). Accumulation in leaves is caused by a combination of increased biosynthesis and slower oxidation in mitochondria. It is synthesised from glutamate via Δ^1-pyrroline-5-carboxylate (P5C); a reaction catalysed by P5C reductase; P5Cs have been shown to increase in response to drought stress (Samaras *et al*., 1995).

Garcia *et al*. (1987) reported that free proline levels significantly increased in maize seedlings in response to water stress. Progressive water stress imposed on wheat also resulted in increased proline and glycine-betaine accumulation (Naidu *et al*., 1990). Ronde *et al*. (2000) detected that with decreasing water content, there was a progressive increase in free proline in six cotton cultivars. Proline accumulation has a role in plant acclimation to water stress and, depending on plant and variety, it may be used as an index for drought stress tolerance.

Presently, there is a debate on lack of clarity on the function of the drought-induced accumulation of proline. Hanson *et al*. (1977) hypothesised that proline accumulation could be a symptom of damage. Ibarra-Caballero *et al*. (1988) observed an increase in proline accumulation in maize varieties exposed to water stress; they concluded that proline accumulation was a symptom of drought and not an adequate characteristic for drought stress resistance. Positive roles for proline have been suggested, including stabilisation of macromolecules, a sink for excess reductants, and a store of carbon and nitrogen for use after relief of water stress (Smirnoff & Stewart, 1985; Smirnoff & Cumbes, 1989; Samaras *et al*., 1995). Verslues and Sharp (1999) suggested that because of high concentrations of proline often observed under stress, proline has a clear role as an osmoticum.

1.5 Mitigating Some Effects of Drought: Seed Priming

Good crop stand establishment is considered to be essential for the efficient use of resources like water and light (Monteith & Elston, 1983). In the rainfed semi-arid tropics, the balance between water supply and demand is critical (Jones, 1987). Uniform stand establishment is a pre-requisite for cropping success under adverse conditions in order to allow each plant maximum access to limited soil water.

Similarly, vigorous early growth is often associated with better yields (Okonwo & Vanderlip, 1985; Austin, 1989; Carter *et al.,* 1992). Harris (1992) demonstrated the importance of germination and emergence to be completed quickly in semi-arid environments. In 9 sowings, made under optimal conditions of soil moisture throughout the 1990-91 season, final emergence and seedling dry weight 25 days after sowing (DAS) varied widely with no discernible relation with date of sowing. The weather after each sowing was different, however, and establishment success varied with the degree of drought stress encountered during the post-sowing period, with 4 out of 9 sowings resulting in poor establishment. Both final emergence and seedling dry matter 25 DAS were highly correlated with the rate of emergence ($r=0.96$ and $r=0.93$, respectively).

A simple approach to speeding up germination is to enhance the genetic potential of seed by treating it in some way before sowing. Various seed treatments are well established, particularly in the horticultural industry and some techniques are quite complicated (Heydecker & Coolbear, 1977). One of the simplest techniques are the

soaking of seed in water for a short period of time prior to sowing (hydro-priming). This method, however, has not been tested systematically for small-grained cereals, although the practice is often used with maize e.g., in Malawi and Zimbabwe.

In a series of controlled environment experiments Harris (1992) showed that the time taken for sorghum seeds to germinate at 30℃ decreased as the soaking time increased from 0 to 10-12 hours, a treatment in which a 50% saving in time could be achieved. Emergence from soil at 30℃ was significantly hastened by 23% when seeds were pre-soaked for 6 hours or longer. In four sowings in the field, soaking sorghum seed for twelve hours before sowing resulted in over 80% better emergence and plants, 25 days after sowing were nearly 60% larger with better developed root systems (Harris *et al*., 1992). The technique of hydro-priming has been used successfully in many other crops and could prove an answer to the problem of poor establishment caused by water stress.

1.6 Justification

The importance of maize as a source of food is undoubted. Since the introduction of maize into southern Africa more than 100 years ago, maize landraces have been subjected to natural and farmer selection under different cultural and environmental conditions. As a result of this selection, many different types of varieties exist, possessing varying levels of adaptability to specific agro-ecological production.

Presently, little or no formal attempts have been made to examine the impact of smallholder farmer selections on adapting maize to different environments or evaluating the current diversity that has resulted from over a hundred years of farmer and natural selection in southern Africa. According to Blum and Sullivan (1986), farmers' local varieties may possess some unique physiological attributes that may not be present in germplasm not exposed to abiotic stress; making them a potential key genetic resource.

A review of literature showed that current research leaned heavily on developing hybrids that are more drought-tolerant. Drought resistant hybrids and their composites are often more promising in dryland environments than local maize varieties (Obeng-Antwi *et al.*, 2002). As such, emphasis has been placed on characterizing hybrids to their level of tolerance for easy selection by farmers or farmer groups. Hence, most literature (if not all) describes the performance of hybrids or improved varieties growing in benign environments.

However, most landraces are grown on marginal lands under dryland conditions by farmers with little or no access to inputs. Under this system, drought through insufficient rainfall and poor rainfall distribution during crop growth is one of the most important stresses affecting production and is the most important source of variations in yield over time (Byrne *et al.*, 1995). The physiological responses of landraces under these conditions are not well understood and, elucidation may offer opportunities for further crop improvement and better agronomic practices.

Global climate change is now generally considered to be underway (Hillel & Rosenweig, 2002), and is expected to result in a long-term trend towards higher temperatures, greater evapotranspiration and an increased incidence of drought in specific regions. Rainfall is likely to be reduced by 5% to 10%, accompanied by a projected increase in temperatures of about 1℃ to 3℃ (Hassan, 2006). These trends, coupled with an expansion of cropping into marginal production areas, are generating increasingly drought-prone maize production environments. An understanding of water use of maize landraces could prove a vital key for sustainable future crop improvements.

There is some debate on whether maize landraces should be classified as an under-utilized crop or traditional crop. By definition, *under-utilized* crops are also *under-researched* crops (Azam-Ali, 2009). The fact that there has been limited research on maize landraces qualifies it as an under-utilized crop. The mechanisms by which maize landraces perform in hostile environments are least understood and/or described. However, it is these mechanisms that are increasingly of relevance for all

agricultural crops that must operate in the vulnerable and volatile environments of the future (Azam-Ali, 2009).

In addition, the fact that much focus has been placed on developing hybrids built for drought tolerance than on characterizing local maize landraces for drought tolerance creates a gap in literature to justify a study along these lines. Maize landraces are still very popular amongst traditional, subsistence farmers who still use it and keep it for consecutive planting seasons. Such a study would aid to the improvement of food security within this vulnerable group which has been left exposed due to their inability to cope with global warming and climate change.

Furthermore, as scientists, we have a moral obligation to not only protect but to also develop indigenous and traditional natural resources such as maize landraces for the benefit of the traditional, rural farmers who still use them and for the preservation of genetic biodiversity.

1.7 Aims and Objectives

The aim of the study was to compare drought tolerance of landraces to two popular hybrids, SC701 and SR52, with respect to early establishment, physiological responses, growth and yield using both controlled environment and field experiments. The study also sought to look at the efficacy of seed enhancements in improving tolerance to drought in landraces.

1.7.1 Specific Objectives

- To compare the popular cultivars and local germplasm with respect to emergence and early establishment performance under drought stress.
- To observe and compare the physiological responses of landraces to drought at the establishment stage.
- To measure and compare the effect of water stress under controlled conditions at different crop growth stages in the local maize germplasm and the popular cultivars.
- To compare the effect on yield in the field achieved with the local maize germplasm and the popular cultivars under varying conditions of water stress imposed by planting at different times during the season.

1.7.2 Hypothesis

Landraces are more drought tolerant than the selected hybrids under both controlled and field conditions.

References

(See final reference section, pages 111-142)

CHAPTER 2a

EARLY ESTABLISHMENT PERFORMANCE OF LOCAL AND HYBRID MAIZE UNDER TWO WATER STRESS REGIMES

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Abstract

Maize (*Zea mays* L.) is the major grain crop in South Africa where most subsistence farmers still plant landraces. The objective of this study was to compare two landrace selections of maize with two hybrids popular among small-scale farmers in KwaZulu-Natal, for seed performance and water stress tolerance during seedling establishment. Two variations of a local landrace, white (Land A) and dark red (Land B), were compared to two hybrids, SC701 and SR52. Standard germination test and electrical conductivity were used to assess seed quality under laboratory conditions. Seedling emergence was performed in seedling trays using pine bark at 25% and 75% field capacity (FC), respectively, over a period of 21 days. All seed types showed high germination capacity (>93%). There were highly significant differences ($P<0.001$) among seed types with respect to daily germination and germination velocity index

(GVI). Landraces germinated slower than the hybrids. Landraces showed a 20% better root length and 41% lower electrolyte leakage than hybrids. There were differences ($P<0.001$) in seedling emergence between 25% FC and 75% FC. Hybrids showed better emergence at 75% FC. At 25% FC seedling emergence was drastically reduced (<5% in all varieties). Hybrids emerged faster than the landraces in both water regimes. Landraces performed better than hybrids under stress conditions. This study showed that landraces may have the same viability as hybrids and a better tolerance to stress during early establishment of the crop.

Keywords: Conductivity, emergence, germination, hybrids, landraces

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Introduction

Many subsistence farmers in South Africa still use local varieties. Whereas these varieties have poorer yield than hybrids under optimum management conditions, they remain an important resource for germplasm improvement (Modi, 2004). Therefore, it is not surprising that many subsistence farmers in South Africa still use landraces.

Drought stress is one of the most important limiting factors in rainfed agriculture and can significantly influence plant performance (Fischer *et al.*, 1978; Ludlow & Muchow, 1990; Turner, 1991). It determines time of germination (Ratcliffe, 1961; Prusinsiki & Khan, 1990; Braccini *et al.*, 1996), influences growth rate and root:shoot ratios and can affect both the final level and rate of germination (Doneen & MacGillavray, 1943). Seedlots vary in their ability to overcome this stress (Guy, 1982) and emerge.

The establishment stage of the crop consists of three parts: germination, emergence, and early seedling growth. When seeds are placed in soil, germination can only be observed as emergence, which may be affected by the water content of the soil (Katerji *et al*., 1994). Early emergence and stand establishment is considered to be one of the most important yield contributing factors. Crop establishment depends on an interaction between seedbed environment and seed quality (Khajeh-Hosseini *et al.*, 2003).

The quality of seed has a profound effect on crop production (Savage, 1995). There has been a wealth of papers reporting the result of differences in seed quality on seedling emergence and crop yield in a wide range of species, including maize

(Perry, 1972, 1976, 1980a, 1982; Powell *et al.*, 1984; Powell, 1988; TeKrony & Egli, 1991). Field emergence is the aspect of seed quality of concern to growers (Pieta Filho & Ellis, 1991).

Seedling emergence is the result of an interaction between seed quality and the often hostile seedbed environment. Under these conditions, chances of successful seedling emergence are greatly influenced by seed quality. Components of seed quality include viability and potential performance (Coolbear & Hill, 1988). Any complete assessment of these should consider the capacity of the seed to produce normal seedlings, and expected field emergence and uniformity (vigour) (Hampton, 1995). Seed quality affects the ability of seeds to overcome the variable conditions experienced by seed during crop establishment. The pattern of seedling emergence resulting from an interaction between seed quality and the environment can be summarized by three parameters:

i. the number of emerged seedlings (crop density),
ii. the mean time of seedling emergence, and
iii. the spread in time to emergence of individual seedlings (uniformity) (Savage, 1995).

Water stress has been reported to increase the accumulation of free radicals in plants. As a reaction to this, oxygen scavenging antioxidant enzymes can be produced to remove those active oxygen radicals (Wang *et al.*, 2002; Sun *et al.*, 2003). Catalase (CAT) is an antioxidant produced by higher plants in response to abiotic stress and metabolises hydrogen peroxide (H_2O_2) into H_2O (Bowler *et al.*,

1992; Noctor & Foyer, 1998). Studies have indicated that activities of antioxidant enzymes are correlated with plant tolerance to abiotic stresses. Drought induced damage was negatively correlated with the capacity of super-oxide dismutase (SOD) and CAT activities in mosses differing in drought tolerance (Dhindsa & Matowe, 1981), rice (Dioniso-Sense & Tobita, 1998; Srivalli *et al.*, 2003; Vaidyanathan *et al.*, 2003) and tomato (Mittova *et al.*, 2003). Therefore, CAT activity is a key factor in understanding maize tolerance to water stress during crop establishment.

Based on Zeven's (1998) definition of a landrace, maize landraces may be described as crop genetic resources that have evolved continuously under natural and farmer selection practices rather than in the collection of gene banks or plant breeding programs. There is presently limited literature describing germination and establishment of maize landraces. If seedling emergence is poor, crop yield will be reduced, and in most situations no amount of effort and expense later in crop development can compensate for this effect. This study aimed to compare the early establishment performance of a local landrace to two popular hybrids under two different water stress regimes, with respect to viability, vigour and physiological responses.

Material and Methods

Seed from indigenous landraces was obtained from local farmers in KwaZulu-Natal. The seed was characterized according to difference in kernel colour. Two colours were selected for this study: white (Land A) and dark red (Land B). Local farmers do not differentiate between kernel colour when planting. However, seed colour has

been shown to have an effect on vigour (Modi, pers. comm.). Two hybrids, popular amongst the small-scale farmers were used: SR52 and SC701, both late maturing varieties with fairly good drought tolerance. Local maize landraces are known to be late maturing (Modi, pers. comm.).

Standard Germination (SG) Test

Four replicates of 25 seeds from each genotype were germinated between double layered paper towels. The rolled papers were put in sealed plastic bags to avoid moisture loss and incubated in a germination chamber at 25℃ AOSA (1992) for 8 days. Daily readings were based on defining germination as radicule protrusion. Observations for final germination percentage, based on normal seedlings, were made according to AOSA (1992) guidelines. Root (longest root) and shoot length, root:shoot ratio and dry matter were measured.

Germination velocity index was calculated according to Maguire's (1962) formulae:

$$GVI = G_1/N_1 + G_2/N_2 + \ldots + G_n/N_n$$

Where:

GVI = germination velocity index

G_1, $G_2 \ldots G_n$ = number of germinated seeds in first, second… last count.

N_1, $N_2 \ldots N_n$ = number of sowing days at the first, second… last count.

Mean time to germination (MGT) was calculated according to the formulae by Ellis and Roberts (1981):

$$MGT = \frac{\sum Dn}{\sum n}$$

Where:

MGT= mean germination time,

n= the number of seed which were germinated on day D, and

D= number of days counted from the beginning of germination.

Electrolyte Leakage (EC)

Electrolyte leakage was measured using the R&A CM100 Model Single Cell Analyzer. 100 seeds from each genotype were individually weighed and put into cells, each filled with 2 ml pure water. Seed of SR52 and SC701 were first rinsed in ethanol to remove the seed coating before being weighed and put into the tray. Electrolyte leakage for each variety was then measured over a period of 24 hours.

Seedling Emergence

Three replicates of 20 seeds from each genotype were planted in seedling trays using pine bark at 25% and 75% field capacity, respectively, over a period of 22 days. The trays were weighed and watered at two-day intervals to maintain field capacity. Data collected included daily emergence for 21 days, seedling height and leaf number (measured once every week), leaf area, root and shoot mass (fresh and dry), and root and shoot length.

Mean time to emergence was calculated using the formulae by Bewley and Black (1994):

$$\text{MET} = \frac{\sum(fx)}{\sum f}$$

Where MET= mean emergence time,

f= number of newly germinating seeds at a given time (day), and

x= number of days from date of sowing.

Protein Electrophoresis and Blotting

Shoots were ground to a fine powder in a pre-chilled mortar under liquid nitrogen (N_2). Samples of 0.5 g were mixed in 5 mℓ Tris-HCl buffer (pH 7.4) containing 250 mM NaCl, 25 mM EDTA, 0.5% (w/v) SDS 10 mM β-mercaptoethanol and centrifuged (15000 rpm for 15 minutes) at 4℃. The supernatants were collected and considered as leaf protein extract. Protein concentration was determined by absorbance at 595 nm (Bradford, 1976) with bovine serum albumin as standard. The supernatant were separated using 10% SDS-PAGE (Laemmili, 1970) and gel electrophoresis was performed with same amount of protein. Western blot was performed with polyclonal catalase antibodies.

Description of Statistical Analysis

Data collected was analysed using GenStat® Version 11 statistical package. One-way ANOVA was used for SG-test and EC-test. Means were separated using LSD $_{(P = 0.05)}$.

Results

Standard Germination Tests

Table1. Performance of landraces (Land A and Land B) and hybrids (SC701 and SR52) during a standard germination test.

Variety	Final Germi-nation (%)	GVI	MGT (days)	EC (*µ*S/g)	Root length (mm)	Shoot length (mm)	Root: shoot	Dry mass (g)
Land A	98a	25.12d	5.075a	90b	91.8ab	53.4b	1.873a	0.3810a
Land B	95a	28.54c	4.9b	117b	114.4a	87.0a	1.432ab	0.3260bc
SC701	94a	31.38b	4.7c	384a	95.7ab	73.3a	1.293bc	0.2940c
SR52	97a	38.12a	4.475d	119b	71.4b	83.7a	0.852c	0.3760ab
$LSD_{(P=0.05)}$	**6.74**	**0.796**	**0.1162**	**123.5**	**27.97**	**16.77**	**0.5156**	**0.05721**

Note: GVI = Germination velocity index; MGT = Mean germination time; EC = Electrical Conductivity. Values not sharing the same letter in the same column differ significantly at $P<0.05$.

Results for the standard germination test (Table 1) showed no differences (LSD $P>0.05$) in final germination percentage, root length, root:shoot ratio (length) and dry mass. Landraces had, on average, a 35% higher root:shoot ratio than the hybrids. Landrace A and SR52 had the highest dry mass, respectively; while on average landraces had 5% more dry mass than the hybrids (Table 1). There were significant differences ($P<0.05$) in shoot length. Landrace B had the highest shoot length.

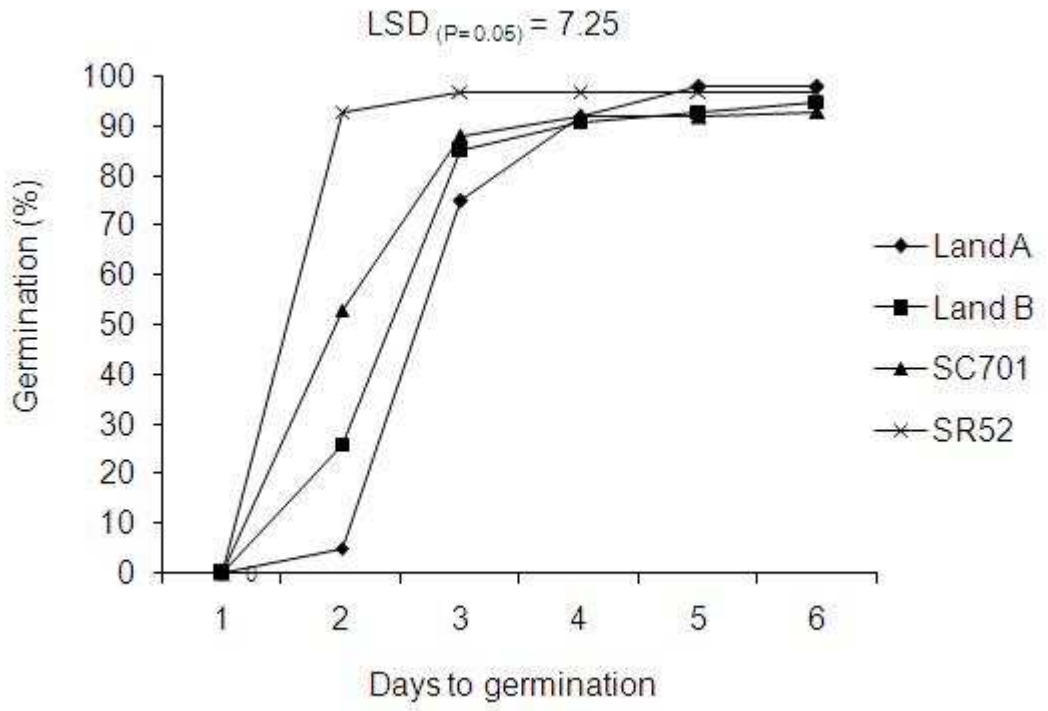

Figure 1: Progress in daily germination percentages of landraces (Land A and Land B) and hybrids (SC701 and SR52) during the first six days of germination inside a germination chamber.

However, there were highly significant differences ($P<0.001$) in daily germination (Fig 1), germination velocity index (GVI) and mean germination time (MGT) (Table 1). Hybrids germinated 23% faster (Fig 1) and more uniformly than the landraces but, reached a constant peak quickly at 3 days (Fig 1). Whereas, the landraces germinated slower but continued doing so, with Landrace A ultimately exceeding the hybrids in final germination percentage (Table 1 & Fig 1).

Electrolyte Leakage (EC)

There were highly significant differences ($P<0.001$) in electrolyte leakage (Table 1). Landrace A, Landrace B and SR52 were statistically not different, with SC701 having the highest and significant electrolyte leakage (Table 1).

Seedling Emergence

Results (Table 2) for seedling emergence showed a highly significant interaction ($P<0.001$) between genotype and field water capacity for most parameters measured. Under optimum conditions, 75% FC, SR52 had the highest emergence, while SC701 and Landrace A had the same emergence (Table 2). On average, the hybrids had a 10% distinctive advantage over the landraces, with respect to emergence. All genotypes emerged poorly at 25% FC, failing to reach 5% emergence. Landrace A, however not significant, showed better emergence compared to the other three genotypes (Table 2).

Hybrids emerged faster than landraces under both optimum and water stress conditions (Table 2). Seedling height, leaf number, leaf area and root length were all significantly ($P<0.001$) reduced under water stress (Table 2). Root lengths of Landrace B, SC701 and SR52 decreased under water stress (Table 2). Landrace A was the only exception, with root length increasing under water stress (Table 2). Under optimum conditions, mean values of landraces for shoot length were 18% lower compared to hybrids. Water stress decreased shoot length of hybrids drastically while the decrease in landraces was not as severe, resulting in landraces, on average, having 39% longer shoots than the hybrids (Table 2). Overall, shoot length

decreased under water stress, by 24% in landraces and 62% in hybrids. There were significant differences ($P<0.05$) in root:shoot ratio (length) between field water capacities, with Landrace A and SR52 registering the highest increments (Table 2). Mean values of root:shoot ratio increased under water stress, with hybrids increasing by 45% and landraces by 29%.

Table 2: Seedling emergence and parameters associated with growth of landrace (Land A and Land B) and hybrid (SC701 and SR52) in response to field water capacity (75% FC and 25% FC)

Treatment	Variety	Emergence (%)	MET (days)	Seedling Height (mm)	Leaf No.	Leaf area (cm^2)	Root length (mm)	Shoot Length (mm)	Root: Shoot
75% FC	Land A	76.7a	16.805c	121.7a	3a	32.8ab	44abc	154.7abc	0.292c
	Land B	60b	17.655b	81.3b	2b	29.6b	50a	168.7ab	0.295c
	SC701	76.7a	16.815c	117.7a	3a	39.9ab	43.3abc	181.7ab	0.243c
	SR52	80a	16.059c	125.7a	3a	48.5a	46.7ab	203.7a	0.232c
25% FC	Land A	3.3c	20.309a	38c	1c	16.2c	56.4a	102.3cd	0.565a
	Land B	1.7c	20.381a	48.1c	0.999c	25bc	31.6c	147bc	0.236c
	SC701	1.7c	19.637a	31.7c	0.201c	10.6cd	30.9c	80.8d	0.382bc
	SR52	1.7c	19.982a	35.3c	0.801c	8.1d	33.7bc	71d	0.486ab
LSD (P=0.05)		**10.38**	**0.7672**	**18.66**	**0.9231**	**15.71**	**15.46**	**56.06**	**0.1613**

Note: MET = mean emergence time; Values not sharing the same letter in the same column differ significantly at LSD (P=0.05)

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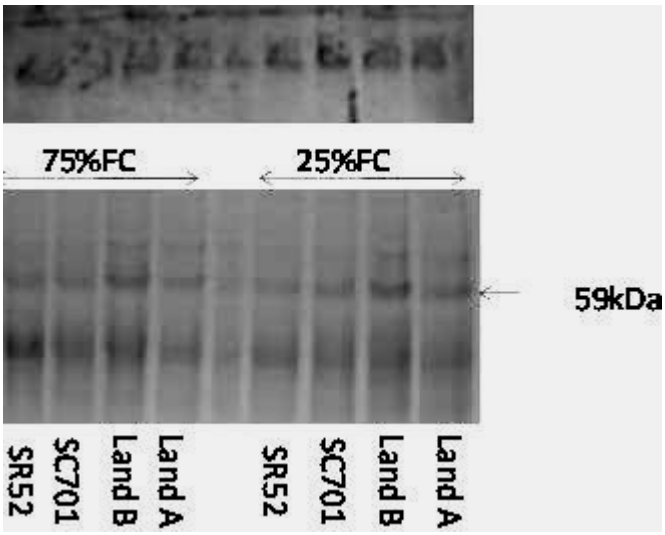

Figure 2: Comparison of protein and catalase expression between landraces (Land A and Land B) and hybrids (SC701 and SR52) in response to two water stress treatments (75% FC and 25% FC).

Protein Electrophoresis and Blotting

In all genotypes, protein was more expressed in the water stressed treatment (Fig 2). Landraces showed more expression than hybrids under both optimum and water stressed conditions. Landrace B, in particular, showed more expression compared to the rest. Blotting showed that catalase was expressed for all genotypes under stress conditions.

Discussion

Sensitivity to water stress adversely affects germination (Wilson *et al.*, 1985) and seed germination is usually the most critical stage in seedling establishment (Almansouri *et al.*, 2001). The standard germination test is used as a measure of viability (ISTA, 1985) with the ultimate objective of gaining information with respect to

field planting value of the seed. Basu (1995) defines seed viability as the property of the seed that enables it to germinate under favourable conditions, provided that any dormancy is removed prior to the germination test. The results showed no significant differences in viability between the landraces and hybrids. However, even when seeds of the same viability are sown at the same time and place, differences in seedling emergence occur (Heydecker, 1972; Perry, 1982). Numerous tests have shown that the SG test is a poor indicator of emergence when field conditions are less than optimal (Dornbos, 1995).

Germination velocity index, according to Carvalho and Nakagawa (1980), indicates the relative strength of a seed lot. Therefore, this strength was limited to hybrids, with SR52 being the fastest. The ability of hybrids to germinate faster and more uniformly could be attributed to hybrid vigour.

The conductivity test is a rapid and well established method of measuring seed quality. It has been developed into a routine vigour test to predict field emergence of garden pea (*Pisum sativum* L.), soybean (*Phaseolus vulgaris* L.) and mungbean (*Phaseolus aureus* Roxb) (ISTA, 1995). SC701 showed higher conductivity than the landraces and SR52. However, conductivity was a poor predictor of emergence in both optimum and water stress conditions.

Seedling emergence is one stage of crop growth that is sensitive to water deficit (Bayoumi, *et al.*, 2008). Emergence was significantly reduced by water stress in all genotypes. On average, the hybrids had higher emergence than the landraces under

optimum conditions, although Landrace A was similar to SC701. Emergence was severely inhibited by water stress in all genotypes. According to Stoskopf (1981), advantages of hybrids are more pronounced under favourable conditions than under non-optimum conditions.

The rate and degree of seedling establishment are extremely important determinants of both crop yield and time of maturity (Rauf *et al.*, 2007). Mean emergence time significantly increased under water stress in all genotypes, although hybrids still emerged faster than the landraces. In the field, the ability of hybrids to emerge faster could give them an advantage as they will be able to start photosynthesizing earlier.

Under conditions of water stress, water uptake by plants is directly related to root growth (Hurd, 1974; Richard & Passioura, 1981) and root development is an important factor determining the adaptability of a plant to water stress conditions (Russell, 1959). Water stress significantly reduced root length in all genotypes, with hybrids being worst affected, decreasing by 33%, on average. Midaoui *et al.* (2003) observed that root length of sunflower was reduced by water stress. Loresto *et al*. (1989), working on rice, found that root length was positively and significantly correlated with drought resistance.

Plant height was significantly reduced by water stress together with leaf area and leaf number. Hutcheon and Ranie (1960) noted that the occurrence of drought at the vegetative stage caused reduction in plant growth and leaf number. Under stress conditions, root and shoot lengths of hybrids decreased by an average of 47.5%

compared to 12.65% in landraces. Although root growth was affected by water stress for all genotypes, it was much less inhibited than shoot growth and concurred with the findings of Sharp *et al*. (1988).

Water stress triggers the plant's defense systems in order to resist oxygen damage caused by oxygen radicals (Ti-da *et al.,* 2006). All genotypes expressed catalase under water stress, confirming that the response was triggered. Landrace B showed more CAT expression and might show a better response to oxidative damage caused by water stress.

Conclusion

Seed performance and seedling establishment are important determinants of crop germplasm performance. Although hybrids performed better, Landrace A sometimes did as well as SR52 and often better than SC701, while Landrace B was often similar to SC701. Overall, this study showed that landraces may have the same viability as hybrids and better tolerance to water stress than hybrids during early crop establishment, but it cannot be concluded that landraces would perform better than hybrids under field conditions. Strength of hybrids was mainly confined to its ability to germinate and emerge faster than landraces. Future studies will investigate performance of landraces and hybrids under a wide range of field conditions, including hydro-priming with a view to improving germination speed and emergence of landraces. It will also focus on identifying and qualifying the proteins expressed as well as the antioxidant capacity and proline accumulation.

References

(See final reference section, pages 111-142)

CHAPTER 2b

Short communication

EVIDENCE OF PROLINE ACCUMULATION IN LEAVES OF MAIZE LANDRACES SUBJECTED TO WATER STRESS

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Abstract

Proline accumulation has been shown to be a widespread plant response to water stress. However, its accumulation in local maize landraces has not yet been studied. Two variations of a local germplasm, white (Land A) and dark red (Land B), were compared to two hybrids, SC701 and SR52. Maize seedlings were grown in seedling trays under controlled environment using pine bark at 25% and 75% field capacity (FC), respectively, over a period of 21 days. Proline accumulation was measured from seedling leaf samples. Results showed rapid proline accumulation in response to water stress. There were highly significant differences ($P<0.001$) between varieties. SC701 and SR52 had the highest proline accumulation, respectively, in response to water stress, compared to Landrace A and Landrace B. Based on previous work, it is

concluded that proline accumulation in leaves of maize seedlings may be a symptom of drought tolerance rather than resistance. We also concluded that the landraces are more tolerant to water stress at the seedling stage than the hybrids SC701 and SR52 since they accumulated less proline, showing less damage.

Keywords: Hybrids, landraces, proline, water stress

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This short communication is a sequel to a previous study (Chapter 2) which investigated the early establishment performance of local maize landraces and hybrids in response to water stress. Water stress has been shown to induce a lowering in the osmotic potential of crops as a means of maintaining turgor (Jones *et al*., 1981). This is achieved by accumulation of solutes within the plant cell or by decreased cell volume; the former is referred to as osmoregulation. Proline has been shown to accumulate under conditions of water stress (Delauney & Verma, 1993) as a universal response by plants to water stress. Several authors have ascribed to it a role in osmoregulation (Shtreva *et al*., 2008; Samaras *et al*., 1995) and tolerance of water stress (Heuer, 1994).

Several roles have been ascribed to proline, with most of them suggesting a positive role (Smirnoff & Stewart, 1985; Smirnoff & Cumbes, 1989; Delauney & Verna, 1993; Samaras *et al*., 1995; Hare *et al*., 1998). In contrast, others have considered proline accumulation to be a symptom of drought (Hanson *et al*., 1977; Ibarra-Caballero *et*

al., 1988). However, there was a dearth of information on proline accumulation in seedlings of maize landraces.

Refer to Chapter 2, Materials and Methods under Seedling Experiment for plant materials and experimental design. Proline content was determined using the method of Bates *et al*. (1973) with some modifications. Samples of 0.5 g freeze-dried leaf material were homogenized in 10 mℓ of 3% sulfosalycic acid (w/v). The homogenate was centrifuged at 11000 rpm for 10 min at 4℃. 2 mℓ of the supernatant was reacted with 2 mℓ acid-ninhydrin and 2 mℓ of glacial acetic acid in a test tube for 1 hour at 100℃, whereafter the reaction was terminated in an ice bath. The reaction mixture was extracted with 4 mℓ toluene, and vortexed for 15-20 sec. The chromophere containing toluene was aspirated from the aqueous phase, warmed to room temperature and the absorbance read at 520 nm using toluene as a blank. The proline concentration was determined from a standard curve and calculated on a dry weight basis as follows:

[(µg proline/ mℓ x mℓ toluene)/ (115µg/µmole)]/ [(g sample)/5] = µmoles proline/g of dry weight material.

Data were analysed using GenStat® Version 11 and means were separated using LSD $_{(P=0.05)}$.

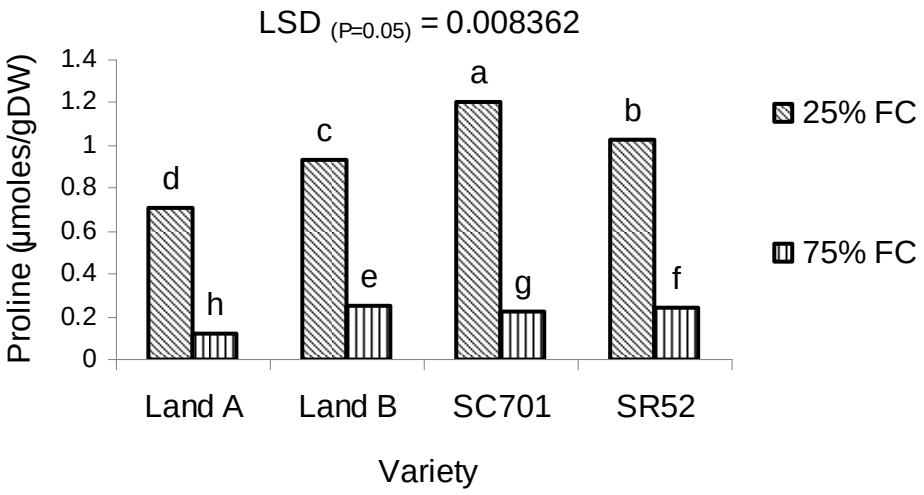

Figure 1: Proline accumulation in leaves of seedlings of landraces (Land A and Land B) and hybrids (SC701 and SR52) under water stress (25% FC) and non-stress (75% FC) conditions.

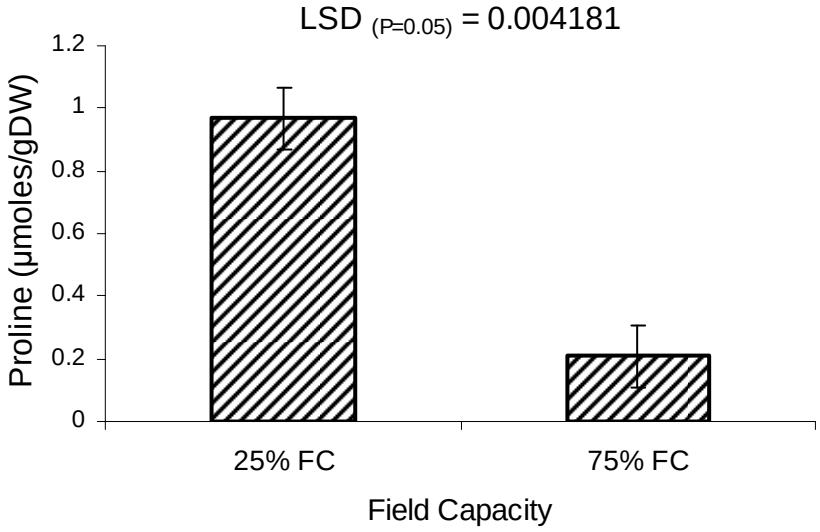

Figure 2: Proline accumulation in leaves of maize seedlings under stress (25% FC) and non-stress conditions (75% FC).

There was a highly significant ($P<0.001$) interaction between field capacity and maize varieties (Fig 1). For all varieties, proline concentration significantly increased under water stress (Fig 2). Landrace B, SC701 and SR52 had the highest concentrations of proline, respectively, under both non-stress and water stress conditions (Fig 1). Under water stress, SC701 and SR52 had the highest concentrations of proline, respectively, compared to Landrace A and Landrace B. Proline concentration was shown to increase sharply in all varieties in response to water stress. Earlier work (Chapter 2) showed that SC701 and SR52 were more sensitive to stress at the seedling stage than the landraces. Thus, in this instance, proline accumulation may be regarded as a symptom of drought stress rather than as an indicator of tolerance to water stress. There have been similar reports showing proline accumulation in plants as a symptom of water stress and not an indicator of stress tolerance (Hanson *et al*., 1977; Aspinall & Paleg, 1981; Ilahi & Dorffling, 1982; Ibarra-Caballero *et al*., 1988). These results concur with previous reports (Chapter 2) that landraces may have a better tolerance to water stress than hybrids (SC701 and SR52) at the establishment stage.

References

(See final reference section, pages 111-142)

CHAPTER 3

EFFECT OF SIMULATED DROUGHT UNDER CONTROLLED CONDITIONS ON GROWTH OF LOCAL MAIZE LANDRACES AND TWO POPULAR HYBRIDS

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Abstract

Drought stress is one of the most important abiotic stress factors. It affects plant growth parameters and has been shown to reduce photosynthesis, and ultimately reducing yield. The effect of drought stress on growth, photosynthesis and yield of local maize landraces has not been studied, although landraces still remain popular amongst local small-scale farmers. This study aimed to investigate the effect of drought on growth, photosynthesis and yield components of a local maize landrace in comparison to two popular hybrids (SC701 and SR52). The landraces were characterized into two separate colours, white (Land A) and dark red (Land B). The experiment was carried out in large pots filled with soil under controlled environment conditions with two water treatments, 25% and 75% field capacity,

respectively. Measurements of emergence, plant height, leaf number, chlorophyll fluorescence and yield components were taken. Results showed no significant differences ($P>0.05$) between field capacities in emergence, mean emergence time, leaf number, chlorophyll fluorescence, ear prolificacy and ear length. Drought had an effect ($P<0.05$) on ear mass, lines per ear, kernels per ear and total grain mass. While landraces had better emergence under water stress, the hybrids achieved a higher yield. We conclude that the effects of drought were more pronounced on yield components than during vegetative growth and that drought had no effect on photosynthesis.

Keywords: Emergence, hybrids, landraces, chlorophyll fluorescence, yield

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Introduction

Drought is a worldwide problem and continues to pose a serious constraint to global crop production. Recent global climate change has made the situation more serious as the frequency and severity of droughts has increased (Pan *et al.,* 2002; Halder & Burrage, 2004). Maize is the staple food crop of South Africa where maize landraces are still very much a part of the traditional cropping system in KwaZulu-Natal. The major reason for crop failure is usually drought through insufficient rainfall and poor distribution during growth.

Effects of drought may vary depending on the growth stage at which drought occurs (Abo-El-Kheir & Mekki, 2007) and extreme water stress at different stages of crop development has been reported to reduce yield significantly (Dhillon *et al*. 1995). Occurrence of drought stress at sowing reduces seedling germination and emergence (Anda & Pinter, 1994). The reduction in growth during the vegetative stage is mainly due to the influence of drought on leaf expansion (Kramer, 1983; Brar *et al*., 1990). After emergence, plants respond to drought stress by reducing stomatal conductance, thus reducing water loss. Reduced leaf turgor inhibits leaf expansion. This, in turn, leads to an increase in assimilate supply to the roots and increased root growth at the expense of above ground growth. Khan *et al.* (2001) found that maize stem height, leaf number and area as well as yield were reduced by water stress.

The reproductive stage of maize is particularly sensitive to water stress (Boyer, 1992). Drought stress delays anthesis and maturation, thus increasing crop

duration (Donatelli *et al*., 1992; Khannachopra & Kumari, 1995). Previous studies have reported that stress during tasseling and silking was most harmful and that stress during grain filling was more drastic than stress during the vegetative stage (Grant *et al*., 1989). Other studies, however, showed that stress during early vegetative growth was more drastic than that during the grain filling stage (Ahmed & Mekki, 2005). In maize, total reproductive failure may result even from brief periods of drought stress at critical stages of plant development (Young & Long, 2000).

Grain yield is dependent on kernel set and the rate and duration of grain-filling (Maiti, 1996). Developing ovaries are weak sinks and may fail if there is insufficient new photosynthate for its growth (Schussler & Westgate, 1991; Bassetti & Westgate, 1993). Alternatively, water stress may prevent ovary fertilisation through reduced silk receptivity (Bassetti & Westgate, 1993), or low water potential may result in premature cessation of kernel growth (Grant *et al*., 1989; Schussler & Westgate, 1991). Drought may also result in reduced assimilate for grain-filling (Young & Long, 2000) resulting in lighter kernels. Under such circumstances, yield can be very significantly low.

Drought has been shown to reduce maize yield by reducing the efficiency with which absorbed photosynthetically active radiation (PAR) is used by the crop to produce new dry matter (radiation use efficiency, RUE) (Earl & Davis, 2003). For C_4 species such as maize, chlorophyll fluorescence (CF) may be used to measure instantaneous leaf RUE under current PAR (Edwards & Baker, 1993; Earl &

Tollenar, 1998). In recent years, CF measurements have become ubiquitous in plant ecophysiology studies (Maxwell & Johnson, 2000). It has been shown that drought stress enhances inhibition of electron transport (Masojidek *et al*., 1991; Giardi *et al*., 1996; Lu *et al*., 2002). Vazan (2002) reported that drought stress reduces variable fluorescence (F_v), initiative fluorescence (F_o) and quantum yield (F_v/F_m) of photosynthesis. Early studies reported a sustained decrease in F_v/F_m of dark-adapted leaves together with an increase in F_o, indicating the occurrence of photoinhibitory damage in response to high temperature (Gamon & Pearcy, 1989) and water stress (Epron *et al*., 1992). Tollenaar and Aguilera (1992) confirmed the role of achieving high photosynthetic rates in crops by showing that observed differences in dry matter accumulation between old and new hybrids were due to higher photosynthetic rates after silking for newer hybrids. It has been noted that the degree of reduction in photosynthesis due to water stress is genotype specific (Sanchez *et al*., 1983; Dwyer *et al*., 1992; Aguilera *et al*., 1999).

Landraces may have “acquired” drought tolerance through years of farmer selection in some of the most adverse of conditions. As water resources for agronomic uses become more limited (Wesley *et al*., 2002), landraces may be key to future crop production. However, little is known on the effects of drought on the growth, photosynthesis and yield of landraces. Thus, the first objective of this study was to observe the effect of water stress on several growth parameters and the photosynthetic system of the landraces. The second objective was to observe effect of water stress on yield components of landraces. Landraces were

compared to two hybrids, SC701 and SR52, under controlled environment conditions.

Material and Methods

Plant Materials

Seeds from a local maize landrace were initially donated by local farmers in KwaZulu-Natal and multiplied at Ukulinga Farm in the year preceding this study. The multiplied seed was characterized into two kernel colours, white (Land A) and dark red (Land B). Two hybrids, SC701 and SR52, were selected for this study based on their popularity among local farmers.

Controlled environment conditions

The experiment was conducted in large (25 ℓ) pots in a temperature controlled (25℃) tunnel at the University of KwaZulu-Natal, South Africa. The experiment was conducted under simulated drought conditions where temperature, solar radiation (PAR) and relative humidity were monitored electronically using HOBO 2K Loggers (Onset Computer Corporation, Bourne, USA).

Experimental design, potting procedure and water stress treatments

The experimental layout was a completely randomized design (CRD) with two factors: variety (four levels- Land A, Land B, SC701 and SR52) and water stress (25% and 75% field capacity, respectively), with three replicates. 24 large pots were each filled with 20 kg of soil whose field capacity had previously been determined by pot weighing. Three seeds were planted per pot (one in the middle

and one on either side) at a depth of 25 mm. Excess seedlings were thinned soon after emergence to only one plant per pot. After planting the seeds in the pots, and based on the soil's field capacity, the pots were watered to 75% and 25% field capacities, respectively. Soil water content in the pots was monitored gravimetrically. Individual pots were placed on a balance and weighed at two-day intervals. Water was then added to the individual pots until the required soil water content of 75% and 25% FC was attained. In order to account and make corrections for plant mass when watering, a few extra pots with plants separate from the experiment were used to verify calculations and estimates. The experimental pots were randomly rotated at every watering interval.

Fertilization and Pests & Disease Management

Fertilizer application was based on a soil analysis report of the soil used in this study. The following fertilizers were applied; 15 g of 2:3:2 (22) per pot at planting and 26 g of UREA (46% N) per pot as top-dressing at 28 days after emergence. Maize was sprayed with Avigard (Malathion) at 15 mℓ/10 ℓ against aphid 8 weeks after planting.

Chlorophyll Fluorescence (CF)

CF was measured using the Plant Efficiency Analyzer (PEA) manufactured by Hansatech Instruments Ltd, Norfolk, England. Leaves were initially dark adapted (30 min) before measurements were taken. Measurements of Fv/Fm were recorded from PEA and used for analysis.

Description of statistical analysis

GenStat® Version 11 was used to perform analyses of variance and means were separated using least significant differences ($LSD_{(P = 0.05)}$).

Results

Emergence

There were no differences (P>0.05) in final emergence with respect to variety and field capacity (Fig 1). Under optimum conditions (75% FC), only SR52 managed to fully emerge (100%), followed by Landrace A (88.9%), SC701 (77.7%) and Landrace B (66.6%). The opposite was true under water stress (25% FC), with emergence increasing in the landraces, 100% for Landrace A in particular, while emergence declined for hybrids (Fig 1). On average, under optimum conditions, landraces emerged 9% less than the hybrids while at 25% FC they had a 25% advantage over hybrids. There were no significant differences (P>0.05) in mean emergence time (MET) (Fig 2). However, landraces emerged 2% slower than hybrids under optimum conditions while the difference under water stress was negligible (<1%).

There were highly significant differences (P<0.001) in daily emergence with respect to variety and days after sowing (DAS) and field capacities (Fig 3a & b). There was no significant interaction (P>0.05) between field capacity, variety and DAS. Hybrids (SC701 and SR52) had faster and more uniform emergence under optimum conditions (75% FC) while landraces performed better under water stress (25% FC).

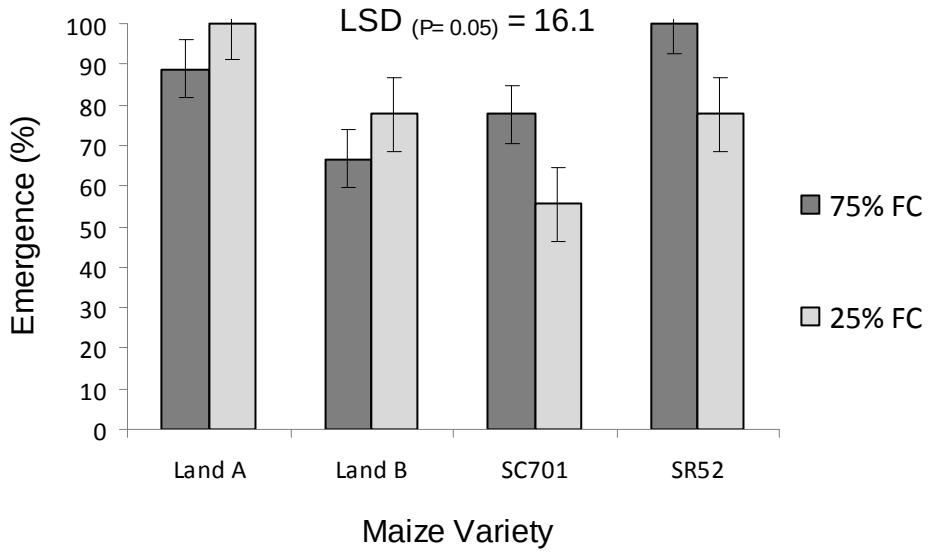


Figure 1: Final percentage emergence of landraces (Land A and Land B) and hybrids (SC701 and SR52) under simulated drought conditions (75% FC and 25% FC).

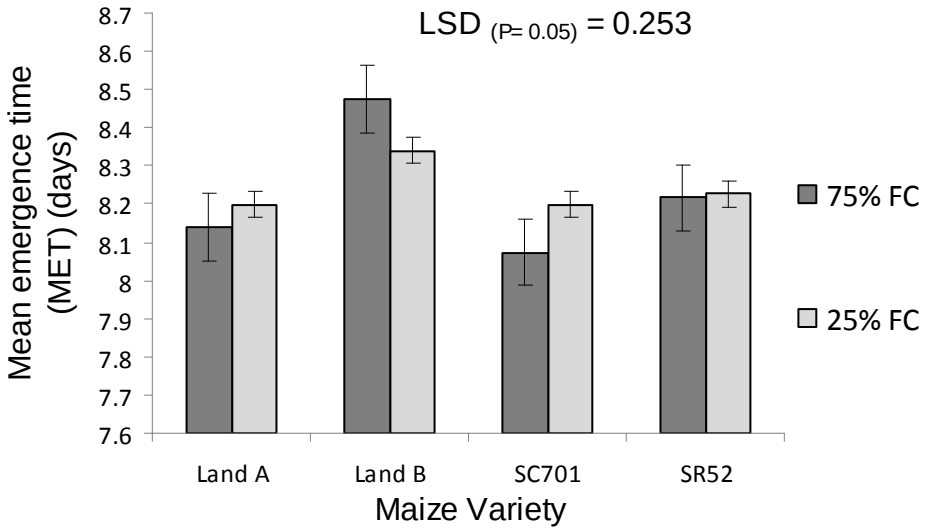
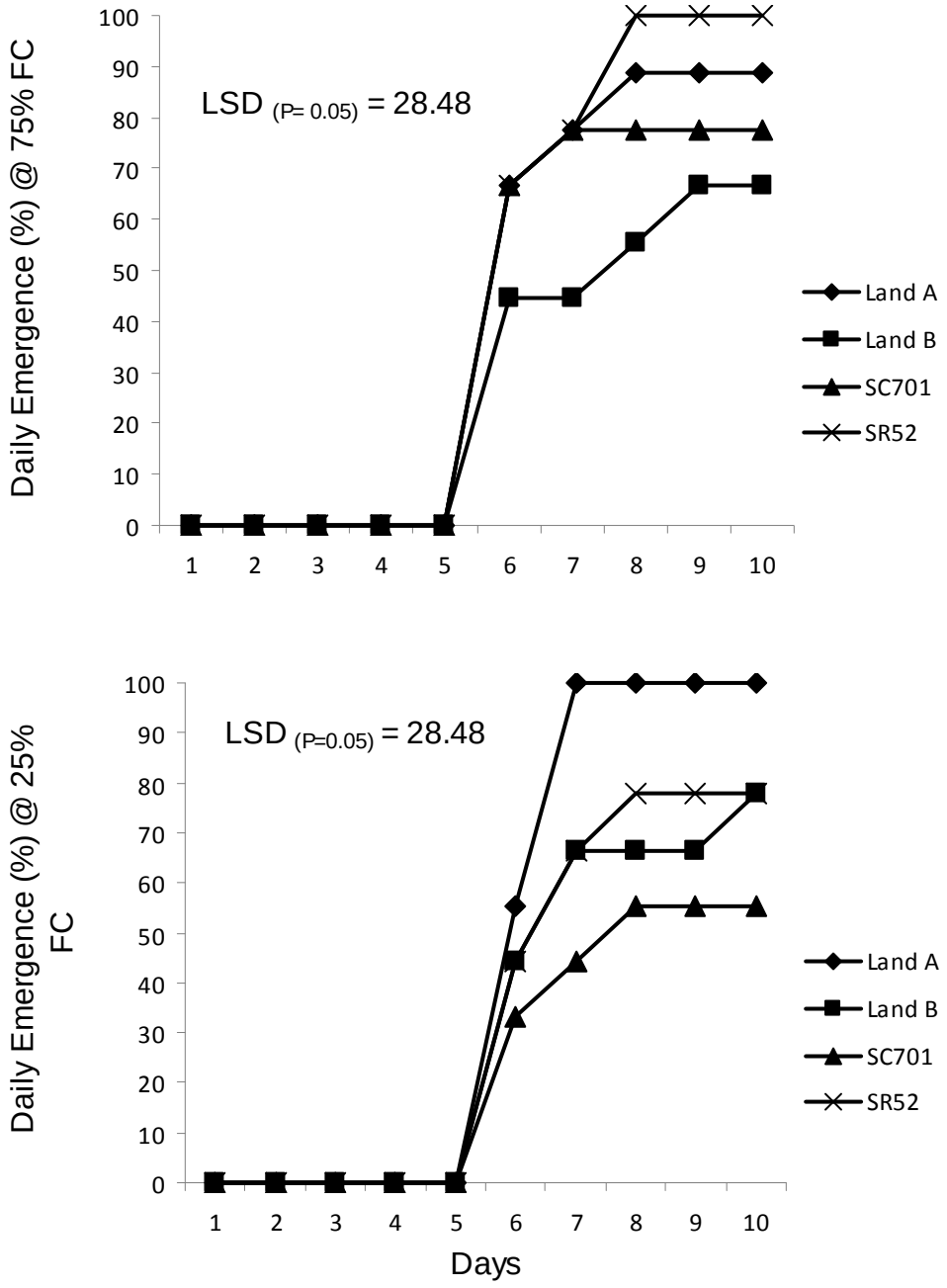


Figure 2: Comparison of mean emergence times (MET) of landraces (Land A and Land B) and hybrids (SC701 and SR52) under simulated drought conditions (75% FC and 25% FC).



Figures 3a and 3b: Progress in daily emergence of landraces (Land A and Land B) and hybrids (SC701 and SR52) during first ten (10) days of simulated drought at 75% FC (3a) and 25% FC (3b).

Plant Growth

There was no significant interaction ($P>0.05$) between field capacity and variety with respect to plant height (Table 1). However, there were highly significant differences ($P<0.001$) between field capacities (Table 1 & Fig 4) with respect to plant height. Under optimum conditions, 75% FC, Landrace B had the tallest plants, followed by SR52 and SC701, respectively, with Landrace A having the shortest plants (Table 1). Plant height for SC701, SR52 and Landrace A were, however, all statistically similar (Table 1). Water stress reduced plant height in all varieties. Landrace B still had the tallest plants, although all varieties were statistically similar (Table 1). Leaf number showed no significant interaction ($P>0.05$) between field capacity and variety. Landrace A and Landrace B increased leaf number under water stress while SC701 was unaffected, with SR52 being the only variety to show a decline in leaf number (Table 1).

Photosynthesis

Photosynthetic efficiency, as measured by CF, showed no significant interaction ($P>0.05$) between variety and field capacity (Table 1). There were slight differences ($P<0.05$) in CF between field capacities (Table 1), with F_v/F_m being higher under water stress as compared to optimum conditions.

Table 1: Plant growth parameters and photosynthetic efficiency of landrace (Land A and Land B) and hybrids (SC701 and SR52) in response to simulated drought.

Treatment	Variety	Height (cm)	Leaf No.	CF (Fv/Fm)
25% FC	Land A	164c	15.67a	0.8303ab
	Land B	191.7c	15.29ab	0.835ab
	SC701	189c	14bc	0.8407a
	SR52	187.7c	13.33c	0.806bc
75% FC	Land A	228b	14bc	0.811abc
	Land B	267.7a	15abc	0.793c
	SC701	238.3ab	14bc	0.8273ab
	SR52	247ab	15abc	0.8103abc
$LSD_{(P=0.05)}$		**34.65**	**1.757**	**0.03342**

Note: CF = chlorophyll fluorescence. Values in the same column not sharing the same letter differ significantly at $LSD_{(P= 0.05)}$.

Under non-stress conditions, SC701 had the highest CF, while Landrace A and SR52 were the same; Landrace B had the lowest CF (Table 1). With the exception of SR52, CF increased in all other varieties in response to water stress. Under water stress, CF for SC701 remained the highest, while Landrace A and Landrace B were the same.

Table 2: Yield components of landrace (Land A and Land B) and hybrids (SC701 and SR52) subjected to drought simulation (75%FC and 25%FC).

Treatment	Variety	Ears/ plant	Ear length (cm)	Ear mass (g)	Kernel rows/ ear	Kernels/ ear	Grain mass (g)
25% FC	Land A	0.67bc	3.5c	2.2c	0d	0b	0b
	Land B	0.67bc	6.33abc	9.5bc	1.33cd	17.7b	8.3b
	SC701	2.33a	11.72abc	15bc	1.17cd	6.7b	5b
	SR52	1.33abc	9.75abc	23.3bc	3.83cd	15.7b	12.8b
75% FC	Land A	1bc	5.83abc	23.9bc	4.67c	48.2b	19.9b
	Land B	0.67bc	8.33abc	50.4b	6bc	75b	39.5b
	SC701	1.33abc	14.5a	118.2a	11a	164.3a	103.1a
	SR52	2.33a	13.03ab	27.3c	1.83cd	21.1b	28.4b
$LSD_{(P=0.05)}$		**1.178**	**8.329**	**46.31**	**4.863**	**82.69**	**46.79**

Note: Values in the same column not sharing the same letter differ significantly at $LSD_{(P= 0.05)}$.

Yield Components

Results of yield components showed no significant interaction ($P>0.05$) between field capacity and variety with respect to ear prolificacy (ears/plant), ear length and kernel number per ear (KNE) (Table 2). Under non-stress conditions, SC701 and SR52 had the longest ears, respectively, with Landrace B and Landrace A trailing, in that order (Table 2). For all varieties, ear length decreased in response to water stress. However, SC701 and SR52 still had the longest ears, respectively (Table 2). Landrace A had the shortest ears under both non-stress and water stress conditions. Under non-stress conditions, 75% FC, SC701 had the highest KNE. Landrace A, Landrace B and SR52 were similar. KNE decreased under water stress conditions. Although all varieties were similar, Landrace A had no kernels under water stress (Table 2).

There was a significant interaction ($P<0.05$) between variety and field capacity, with respect to cob mass and lines per cob (Table 2). SC701 had a significantly higher ear mass under non-stress conditions. Landrace B followed closely while Landrace A and SR52 were similar (Table 2). Ear weight under water stress for SR52 and SC701 was highest and Landrace A had the least ear weight (Table 2). Under non-stress and water stress conditions, mean ear weight of landraces was 49% and 69% lower than hybrids, respectively. SC701 had the most kernel rows per ear, while Landrace A, Landrace B and SR52 were similar, although SR52 had less than 2 lines/ear (Table 2). Mean values of landraces for kernel rows per cob were 16% and 73% lower compared to hybrids under non- and water-stress conditions, respectively. Grain mass followed a similar trend as ear mass, kernel

rows per ear and KNE. SC701 had the highest grain mass per plant, while Landrace A, Landrace B and SR52 were similar under non-stress conditions. Grain mass was reduced by water stress, with SR52 and Landrace B having the highest grain mass under water stress (Table 2).

Discussion

Advantages of hybrids are more expressed under optimum conditions than at sub-optimum conditions (Stoskopf, 1981). Under sub-optimum conditions, landraces may perform better than hybrids because of adaptability and continued selection under such conditions (Zeven, 1998). This was evident as hybrids out-emerged landraces by 9% under optimum conditions but, however, were out-emerged by 25% by landraces under water stress. Ability of landraces to emerge better than hybrids under water stress conditions may be as a result of adaptability brought about from being usually planted in dry seedbeds by communal farmers.

The occurrence of drought at the vegetative stage is known to result in a reduction in plant growth and leaf number (Hutcheon & Ranie, 1960). Landraces, on average, had a 2% advantage over the hybrids under optimum conditions; the opposite was true under simulated drought, with the hybrids having a 5% advantage, with respect to plant height. Drought stress reduced plant height significantly, although all varieties grew very tall under both water stress regimes. Similar results showing a reduction in stem height due to water stress have been reported in other maize varieties (Hernandez, 1980; Porro & Cassel, 1986; Khan *et al*., 2001). Contrary to reports in literature (Ephrath & Hesketh, 1991; Abo-El-

Kheir & Mekki, 2007), results (Table 2) showed that there were no differences (P>0.05) in plant leaf number. Drought, therefore, had no effect on leaf expansion.

In a previously dark adapted leaf, F_v/F_m is representative of the quantum yield of photosynthesis in photosystem two (PSII). For non-stressed plants, this value has been shown to range from 0.75 to 0.85 (Baker & Hellon, 1987; Bolhar-Nordenkampf *et al*., 1989) and to be correlated with net photosynthesis quantum yield in intact leaves (Demming & Bjorkmann, 1987; Comic & Briantais, 1991; Vazan 2002). Drought stress is expected to result in a declining slope for Fv/Fm (Scbreiber & Bilger, 1993; Angelopoulos *et al*., 1996). In contrast, results showed that photosynthesis was not affected by drought stress (Table 1). Instead, it increased under stress. Under both water regimes, F_v/F_m values were above 0.75 on a scale of 1.000, indicating that the photosynthetic capacity of the leaves remained intact under water stress for both landraces and hybrids.

Another reason may be that maize carries out C_4-photosynthesis which is saturated at CO_2 partial pressure levels that are well below the ambient. As such, stomatal closure, caused by water stress, may occur without any significant impairment to the leaf's photosynthetic capacity (Young & Long, 2000). Lal and Edwards (1996) suggested that there could be significant cycling of CO_2 in drought stressed maize leaves, accounting for this phenomenon. Zulini *et al*. (2007) suggested that photosynthetic efficiency may only be affected at a relatively high intensity of drought.

The occurrence of drought at any growth stage has been found to reduce yield (Grant *et al*., 1989; Khan *et al,* 2001; Abo-El-Kheir & Mekki, 2007). For most yield components, landraces, in particular Landrace A, was more affected by water stress as compared to hybrids, whilst hybrids, and in some instances Landrace B, dominated under optimum conditions. Ear length for all varieties decreased under water stress by about 24% on average, while landraces still had smaller ears compared to hybrids under optimum conditions. Drought stress during tasseling and silking may have reduced ear length (Thelen, 2009). Interestingly, even though key yield determinants such as leaf number and photosynthesis were not affected by drought, there was a reduction in yield, with Landrace A, in particular, failing to develop any grains under water stress conditions. According to Nielson (2005), poor kernel set, (meaning an unacceptably low kernel number per ear), is not surprising under severe stress caused by drought. Poor kernel set may have been caused by ineffective pollination as a result of severe water stress (Nielson, 2005).

Conclusion

Drought is an important source of stress which has been shown to reduce plant growth and thereby reduce yields significantly regardless of the time of its occurrence. This study showed that plants were more tolerant to water stress during the early vegetative stages, the landraces in particular. Landraces proved to be more resilient at the seedling stage as shown by its ability to emerge well under water stress. Growth parameters of plant height and leaf number were not affected by water stress. Landraces performed similar when compared to hybrids,

with the only exception being that landraces had more leaves under water stress. Photosynthesis was generally not affected by water stress; it increased under water stress, indicating no damage to the photosystem. However, despite an ability to maintain photosynthesis under water stress, the effect of drought on landraces was more pronounced on the yield components, with Landrace A rendered barren by water stress. Hybrids yielded better than the landraces under both optimum and water stress conditions. This study showed that although landraces may have a degree of water stress tolerance at the early establishment stage, it may not necessarily translate into a sustained advantage throughout growth leading up to yield. Further studies in the field will verify these findings.

References

(See final reference section, pages 111-142)

CHAPTER 4

PLANTING DATE EFFECTS ON GROWTH AND YIELD COMPONENTS OF LOCAL LANDRACES IN COMPARISON TO TWO HYBRIDS UNDER RAINFED CONDITIONS

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Abstract

Little is known on the response of maize landraces to water stress under dryland conditions. The objective of this study was to observe planting date effects in relation to changes in soil water content during the season on growth and yield components of a local maize landrace in comparison to two hybrids. Two colour variations of a landrace, white (Land A) and dark red (Land B) were selected and two hybrids, SC701 and SR52. The experimental layout was a complete randomised design (CRD) with three replications. Three trials were planted on three dates representative of early, optimum and late planting from August 2008 to January 2009. Planting date had highly significant effects ($P<0.001$) on emergence, plant height, leaf number and days to tasseling (DTT). Landraces emerged better than hybrids in all plantings;

highest emergence was in the early and late plantings. Maximum plant height and leaf number were attained in the optimum planting, with early planting having the least heights and leaf numbers. Hybrids were taller and had more leaves than landraces in all plantings. Early planting took the longest number of days to tassel (104 Days after Sowing). DTT decreased with successive plantings. There were no differences ($P>0.005$) between varieties. Planting date had a significant effect ($P<0.05$) on ear prolificacy (EP), kernels/ear (KNE) and 100 grain mass (GM). EP was highest in the optimum and early planting, respectively. KNE was highest in the late planting while 100 GM decreased with successive plantings. Planting date had no effect on ear length and mass, kernel rows/ear, grain mass and yield. With the exception of EP, hybrids performed better than landraces, with respect to yield components. Landraces responded well to optimum and late planting.

Keywords: Drought, hybrids, landraces, planting dates, yield components.

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Introduction

Maize is the major grain crop in South Africa, being the major feed grain and staple food crop for the majority of the population. In KwaZulu-Natal, small-scale farmers still use traditional maize varieties, or landraces, since the cost of hybrid seed is unaffordable for most of them and they can easily recycle seed from the landraces. Their crop is rain-fed and is usually planted in late spring or early summer right through to January. Yields in dryland maize producing areas are constantly reduced by erratic seasonal rainfall distribution (Du Toit, 2002).

Drought, either through low and erratic rainfall amounts or spatial variation is a major feature of the South African climate (SA Weather Services, 2008). As a result, there exists a lot of variation in dryland maize yields (Benhil, 2002). Drought results in water stress due to reduced soil water content and is one of the major causes of yield loss the world over. Maize has been reported to be very sensitive to drought (Farre *et al*., 2000). Sensitivity to water stress varies according to development stage of the plant (Doorenbos & Kassam, 1979). Water stress occurring at different growth stages of maize may reduce final yield by varying degrees. Even minor drought during specific physiological stages can reduce maize yields substantially. The actual extent of yield reduction is dependent upon intensity of water stress as well as the developmental stage at which the stress occurs (Wilson, 1968; Claasen & Shaw, 1970; Heinegre, 2000).

The late spring crop is normally planted before the onset of the rainy season, thus, exposing it to water stress at the establishment stage. The occurrence of water stress

at this stage has been reported to reduce emergence (Mohammadkhani & Heidari, 2008) and plant population. Yield is the collective of individual plant contributions. A low plant population means fewer plants to contribute to yield and thus reduced yield, even though individual plants in the remaining population may still perform well.

The occurrence of drought at the vegetative stage reduces plant height and leaf size. Khan *et al*. (2001) reported reduced plant height in maize exposed to water stress. Short-term water stress immediately reduced the rate of expansion of growing maize leaves although the reduction was overcome following the relief of water stress (Acevedo *et al*., 1971). Impact on yield will thus be the result of reduction in leaf area available for photosynthesis (Heinegre, 2000). There is debate on the sensitivity of maize to water stress at the vegetative stage. Ahmed and Mekki (2005) recently argued that stress at the vegetative stage was more detrimental to yield than stress at the grain-filling stage.

However, there seems to be general consensus that maize is less sensitive to water stress at the vegetative stage than during the reproductive stage (Grant *et al*., 1989; Dhillon *et al.*, 1995). The onset of the reproductive stage is the most sensitive stage for drought stress. Water stress around flowering and pollination delays silking, reduces silk length, and inhibits embryo development after pollination. Drought stress may delay silk emergence until pollen shed is nearly or completely finished. Under such circumstances, severe yield reductions may occur due to incomplete pollination and loss of kernel number (Lauer, 2003).

There have also been several studies on the mechanisms responsible for yield loss under water stress conditions at various growth stages. If drought coincides with tasseling, it may reduce cob size and prolificacy (Heinegre, 2000). Water stress after silking up to maturity affects kernel weight. Drought during the grain-filling period results in a shortened grain-fill period and lowers kernel weight. If soil water content is depleted during the “milk” and “dough” stages of grain-fill, grain abortion may occur (Coffman, 1998). Dry weather that starts early and covers several growth periods may have a compounding effect with severe reductions in maize yield (Heinegre, 2000).

Maximum yields are therefore only attainable if there is sufficient soil water throughout the entire growing season. As a result of variations in yield due to seasonal variations in soil water content, there is need for an understanding of management practices that affect crop performance. Selection of planting dates has been shown to affect maize yield potential and stability (Norwood, 2001). The challenge is to find a narrow window where critical growth stages will coincide with favourable conditions in the field. Sheperd *et al*. (1991) reported that early planting could contribute significantly to higher yields. Otegui and Melon (1997) concurred by reporting that earlier planting tended to place the tasseling and silking period ahead of the risk of water stress and thus recommended earlier planting. They also reported that late planting resulted in less biomass production, reduced kernel set and low grain yield. Delayed plantings are generally accompanied by increased temperatures during the growing season which accelerate crop development and decrease accumulated solar radiation (Otegui & Melon, 1997).

The dependency of most local farmers on rainfed agriculture makes them extremely vulnerable to yield variations. Under field conditions, the variability of rainfall and consequently soil water content means that water stress can occur at any stage of the plant's development and at varying degrees of intensity and length. While hybrids have been tested under varying conditions in the field, there have been no such studies for local maize landraces. Their responses to different planting dates and changing soil water content under field conditions are least understood. This study sought to understand the performance of landraces, in terms of growth parameters and yield components, to different planting dates in relation to changes in soil water content during the season.

Material and Methods

Planting material and field layout

Three field experiments were planted at the University of KwaZulu-Natal Research Farm (Ukulinga) in Pietermaritzburg (29°37'S 30°16' E) under dryland conditions. The long-term mean rainfall and temperatures for Ukulinga are presented in Table 1. The experimental design was a completely randomised design (CRD) with two factors, planting date and variety, with three replications. Two colour variations of local maize landraces, white (Land A) and dark red (Land B) were used in the study, together with two hybrids, SC701 and SR52. There were three planting dates; 28 August 2008 (early planting), 23 October 2008 (optimum planting) and 9 January 2009 (late planting). The plant population was 26 667 plants per hectare (0.75 x 0.5 m).

Table 1: Long-term climatic data (rainfall and temperature) for Ukulinga, Camp (1999).

	Annual	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Rainfall (mm)	738	116	98	92	48	27	10	10	30	51	67	90	99
Temp (℃)	18.1	21.9	21.9	21.1	18.7	16	13.4	13.4	15.2	17.1	18.3	19.5	21.2

Growth parameters

Plant height was measured from the soil surface to the base of the tassel. Leaf number was counted for leaves with at least 50% green area up till flowering. Days to tasseling (DTT) were counted as number of days from sowing to when 50% of the population had tasselled. Yield components were measured at harvest.

Crop management

Weeding was done mechanically. Fertiliser application was based on soil analysis recommendations; 20 kg phosphorus (P) per hectare and 180 kg nitrogen (N) per hectare. All of P was applied at planting in the form of a basal application, using 2:3:2 (22). Plants were top-dressed with UREA (46% N) at 28 days after emergence (DAE). UREA was placed in shallow holes next to plants and covered-up immediately. Kemprin (Cypermethrin @ 12 mℓ/10 ℓ) was used to control aphids**.**

Weather and soil water content

Weather data for the duration of the study (August 2008 to May 2009) was obtained from measurements collected by an automatic weather station (AWS) located about 100m from the study site. Measurements shown are monthly averages compiled from hourly readings. Three samples for soil water content were taken weekly from the 30cm profile throughout the duration of the study. Soil samples were weighed to obtain mass of wet soil and thereafter dried at 80°C until they had reached constant mass. Soil water content was then calculated using the following formula;

$$\text{Soil water content} = [(\text{wet soil} - \text{dry soil}) / \text{dry soil}] \%$$

Data analysis

The experiments were performed in a CRD with three replications. Statistical variance analysis was done using GenStat® Version 11. The ANOVA test was used and means were separated using least significant differences (LSD) at 5%.

Results

Emergence and Growth

Planting date had a highly significant effect ($p<0.001$) on final emergence. While, over-all, there were significant differences ($p<0.05$) between varieties, there was no significant interaction ($p>0.05$) between planting date and variety (Table 2). Landrace A and Landrace B had the highest emergence in the early planting, respectively, with SC701 and SR52 being equal (Table 2). For all varieties, emergence decreased in the optimum planting (Table 2). Although emergence increased in the late planting, it was less than that attained in the early planting, with the exception of Landrace A

which equalled the early planting (Table 2). On average, for all varieties, emergence decreased by 48% and 5% in the optimum and late plantings, respectively, when compared to the early planting. For all three planting dates, landraces (Land A and B) emerged better than the hybrids (SC701 and SR52); on average, emergence of the hybrids was 6% and 17.86% lower than the landraces in the optimum and late planting, respectively.

There were significant differences ($p<0.001$) between planting dates, with respect to both final plant height and leaf number (Table 2). With the exception of Landrace A, all other varieties attained maximum plant height in the optimum planting, followed by late and early planting, respectively (Table 2). Maximum leaf number was attained in the optimum planting, followed by early and late planting, respectively (Table 2). Although earlier planted crops were shorter than the late planted crops, they had more leaves (Table 2). There were no differences ($p>0.05$) between varieties as well as no significant interaction ($p>0.05$) between planting date and variety.

DTT were significantly affected ($p<0.001$) by planting date (Table 2). There were no differences ($p>0.05$) between varieties, as well as no significant interaction ($p>0.05$) between planting date and variety (Table 2). Early planting took the longest number of days to tassel (≈104 DAS) (Table 2). Landrace A, SC 701 and SR52 tasselled at the same time while Landrace B tasselled earlier (Table 2). On average, the optimum and late plantings tasselled 22 days (≈82 DAS) and 26 days (≈40 DAS) earlier than the early planting. For both optimum and late planting, Landrace A, Landrace B and SC701 tasselled at the same time while SR52 took longer to tassel (Table 2).

Table 2: Growth of landrace (Land A and B) and hybrids (SC701 and SR52) for three different planting dates.

Planting Date	Variety	Emergence (%)	Plant Height (cm)	Leaf Number	DTT (DAS)
Early	Land A	93.3a	92.9e	11.88bc	105a
	Land B	86.7ab	88.1e	11.91bc	102.67a
	SC701	74.7bcd	99.3e	12.35bc	105a
	SR52	74.7bcd	168.4de	11.57bc	105a
Mean		**82.3**^{a}	**97.2**^{b}	**11.93**^{b}	**104.42**^{a}
Optimum	Land A	40e	141.1bc	12.78ab	81.67b
	Land B	48e	143.6bc	12.67abc	81.67b
	SC701	38.7e	172.3a	12.89ab	84b
	SR52	44e	163.9ab	13.67a	81.67b
Mean		**42.7**^{c}	**155.2**^{a}	**13**^{a}	**82.25**^{b}
Late	Land A	93.3a	158.8ab	11.67bc	63d
	Land B	78.7bcd	130.4cd	10.74c	63d
	SC701	72cd	146.1ab	11.4c	67.67c
	SR52	69.3cd	142.7bc	10.83c	63d
Mean		**78.3**^{b}	**144.5**^{a}	**11.16**^{a}	**64.17**^{c}
$LSD_{(P=0.05)}$ P.Date		6.79	13.97	0.662	2.288
$LSD_{(P=0.05)}$ PD x Var		13.58	27.95	1.324	4.575

Note: DTT = days to tasseling; DAS = days after sowing. *Numbers with different letters in the same column differ at $LSD_{(P=0.05)}$.

Table 3: Yield components of landrace (Land A and B) and hybrids (SC701 and SR52) for three different planting dates.

Planting date	Variety	Ears/Plant	Ear length (cm)	Ear mass (g)	Kernel rows/ ear	Kernels/ ear	Grain mass/ Plant (g)	100 Grain Mass (g)	Grain Yield (t/ha)
Early	Land A	3.1a	14.05bc	122b	8.41bc	169cd	83.9bc	50.36cd	2.23b
	Land B	2.157a	11.29d	88.4bc	9.35b	153d	76.9bc	45.17d	2.07b
	SC701	1.2c	19.3a	278.5a	9.63b	294b	174.7ab	64.1a	4.67ab
	SR52	1.083c	19.03a	279.8a	10.28ab	354ab	210.5a	62.23ab	5.6a
	Mean	**1.885^{a}**	**15.92^{b}**	**192.2^{a}**	**9.42^{b}**	**243^{a}**	**136.5^{a}**	**55.47^{a}**	**3.64^{a}**
Optimum	Land A	3.333a	14.56bc	150.8b	9.38b	239bcd	121.9b	50.15cd	3.27ab
	Land B	1.611b	14.35bc	131.1b	10.04ab	281bc	112.3b	46.03d	3b
	SC701	1.444b	18.19ab	209.8ab	11.24a	337ab	170.4ab	55.78abc	4.57ab
	SR52	1.167c	20.3a	220.3ab	10.27ab	345ab	191.3ab	53.83bc	5.07ab
	Mean	**1.889^{a}**	**16.85^{ab}**	**178^{a}**	**10.23^{ab}**	**300^{ab}**	**149^{a}**	**51.45^{ab}**	**3.98^{a}**
Late	Land A	1.067c	15.91bc	164.2b	10.07ab	306b	139.4b	44.62d	3.73ab
	Land B	1.229c	14.98bc	134.3b	9.27b	266bcd	129b	46.3d	3.47ab
	SC701	1c	20.74a	242.1a	12.13a	441a	190.5ab	45.6d	5.07ab
	SR52	1.111c	19.11a	223a	10.73ab	379ab	187.5ab	49.47cd	5ab
	Mean	**1.102^{b}**	**17.68^{a}**	**190.9^{a}**	**10.55^{a}**	**348^{a}**	**161.6^{a}**	**46.5^{b}**	**4.32^{a}**
$LSD_{(P=0.05)}$ P.Date		0.4097	1.588	49.88	1.093	59.4	34.63	4.711	0.923
$LSD_{(P=0.05)}$ PD x Var		0.8195	3.176	99.75	2.186	118.8	69.26	9.422	1.846

Note: DAE = days after emergence. *Numbers with different letters in the same column differ at $LSD_{(P=0.05)}$

Yield components

With the exception of ear prolificacy (EP), there were no significant interactions ($P>0.05$) between planting date and variety for all other yield components measured (Table 3). Highly significant differences ($P<0.001$) between planting dates and varieties were observed with respect to ear prolificacy (Table 3). Landrace A and Landrace B had the highest number of ears per plant, respectively, in the early and optimum planting, with Landrace A having at least 3 ears per plant (Table 3). EP decreased in the late planting for landraces. For all three planting dates, landraces had the highest number of ears per plant when compared to the hybrids; on average landraces had at least 2 ears/plant compared to 1 ear/plant in the hybrids (Table 3).

Ear length, for all varieties, increased by 5% and 11% in the optimum and late planting date, respectively, albeit not significantly ($P>0.05$) (Table 3). There were highly significant differences ($P<0.001$) for ear length between varieties. In all three plantings, ear lengths of SC701 and SR52 were significantly longer than ears of Landrace A and Landrace B. Ears of hybrids were 37% longer than ears of landraces. Although ear length of landraces increased in the successive plantings (14% and 22% increments in the optimum and late plantings compared to the early planting), ears remained smaller than ears of hybrids (Table 3).

Planting date had no effect ($P>0.05$) on ear mass (Table 3). However highly significant differences ($P<0.001$) occurred between varieties (Table 3). Ear mass of SC701 and SR52 was significantly higher to ear mass for landraces in the early and late planting (Table 3). The difference was more pronounced in the early planting;

ears of hybrids weighed, on average, a staggering 165% more than ears of landraces. The difference was reduced to an average of 54% more weight in the optimum and late plantings due to the weight gain recorded in ears of landraces; ears of landraces increased weight by 33% and 42%, on average, in the optimum and late plantings, respectively, compared to the early planting (Table 3).

Although not significant ($P>0.05$), kernel rows per ear (KRE) increased with successive planting dates (Table 3). There were however, significant differences ($P<0.05$) between varieties. Landrace B was similar to SC701 in the early planting, while SR52 had the most KRE (Table 3). In the optimum planting, Landrace B was similar to SR52, with SC701 having the most number of lines per ear (Table 3). Landrace A improved in the late planting and was similar to SR52, while SC701 still had the most number of lines per ear (Table 3). Based on mean values, hybrids dominated landraces for all three planting dates; hybrids had an average of 11 KRE compared to 9 KRE in the landraces (Table 3).

Kernel number per ear (KNE) differed significantly ($P<0.05$) between planting dates (Table 3). There were highly significant differences ($P<0.001$) between varieties and no significant interaction ($P>0.05$) between planting date and variety (Table 3) was recorded. For all three plantings, SC701 and SR52 had a much higher KNE than landraces. KNE increased with successive planting dates in the landraces and hybrids, with the exception of SR52 and Landrace B which decreased in the optimum and late planting, respectively (Table 3). Based on mean values, hybrids had a greater KNE (52%) than landraces. As with ear mass, this advantage of hybrids over

landraces was more pronounced in the early planting date; KNE in hybrids was more than double (101%) landraces in the early planting (Table 3).

Grain mass per plant was not significantly affected ($P>0.05$) by planting date, although it increased with successive planting dates, in line with increments recorded in KRE and KNE (Table 3). There were significant differences ($P<0.001$) between varieties. No significant interaction ($P>0.05$) between planting date and variety was observed. SR52 and SC701 had the highest grain yield per plant, respectively, in the early and optimum planting (Table 3). Grain yield increased with successive planting dates in Landrace A and Landrace B, although it still remained lower than SC701 and SR52 (Table 3). The greatest differences were observed in the early planting; average grain mass per plant of hybrids was more than double (140%) that of landraces (Table 3).

Dry matter accumulation was measured as 100 grain mass (100 GM). There were significant differences ($P<0.05$) between planting dates and between varieties (Table 3). There was no significant interaction ($P>0.05$) between planting date and variety. SC701 and SR52 had the highest 100 GM, respectively, in the early and optimum planting (Table 3). Landrace A was similar to SR52 in the optimum planting (Table 3). Landrace B increased with successive planting dates while Landrace A, SC701 and SR52 decreased with successive plantings (Table 3). Consequently, Landrace B had the second highest 100 GM in the late planting, while SR52 had the highest 100 GM (Table 3). Overall, compared to the early planting, 100 GM decreased with

successive planting dates, by 7% and 16% in the optimum and late planting dates, respectively.

Results for total grain yield (t/ha) were consistent with results for yield components measured (ear length and mass, KRE and KNE) (Table 3). There were no differences ($P>0.05$) between planting dates, but highly significant ($P<0.001$) differences between varieties were observed (Table 3). The interaction between planting date and variety was not significant ($P>0.05$). For both Landrace A and Landrace B, grain yield increased with successive plantings, with highest grain yields being achieved in the late planting (Table 3); the opposite was true for SR52. SC701 achieved highest grain yield in the late planting (Table 3). SR52 was consistent in all three plantings (>5 t/ha) (Table 3). Over-all, hybrids out-yielded landraces by 69%. The greatest yield differences (139%) were recorded in the early planting, while the gap narrowed in successive plantings (54% and 40% in the optimum and late plantings, respectively).

Weather and soil water content

Average monthly rainfall amounts measured for the period September to December 2008 showed less than 1mm of rainfall recorded (Fig 1). Monthly soil water content measured over the same period showed averages of less than 20% soil water content (Fig 2). Temperatures during this period were also low; September had the lowest average temperature of less than $10^{o}C$ (Fig 1). This period coincided with the first and second planting dates. Both rainfall and soil water content increased considerably over the period January to May 2009 (Fig 1 & 2).

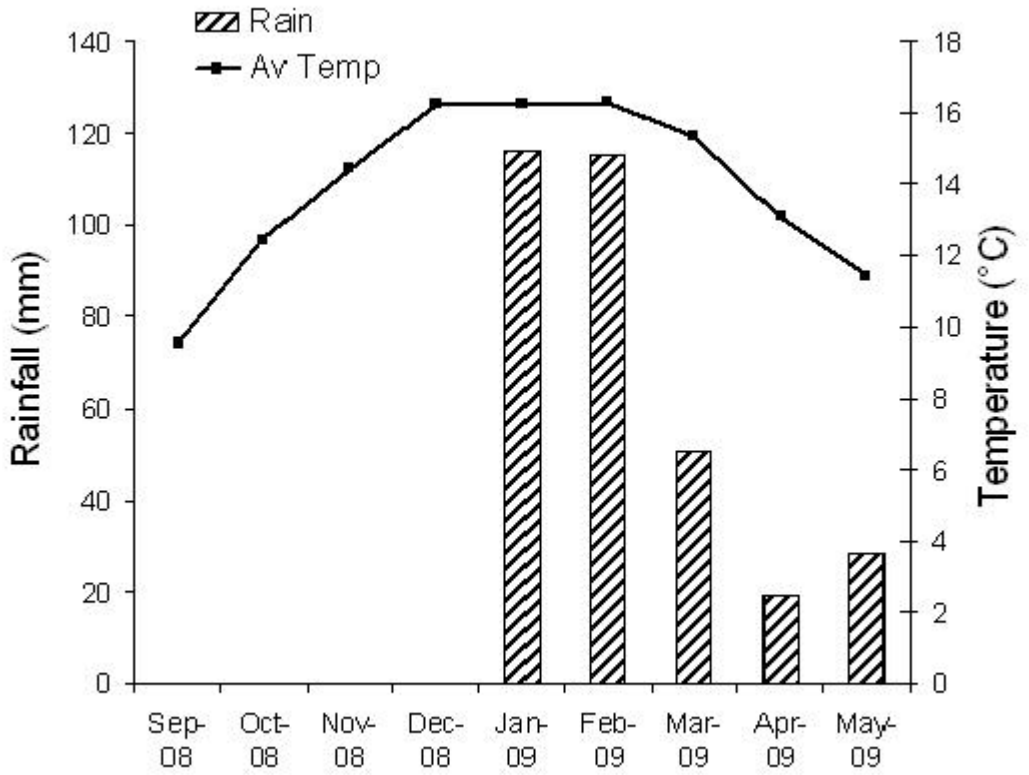

Figure 1: Monthly average rainfall and temperature (℃) recorded at Ukulinga during September 2008 to May 2009.

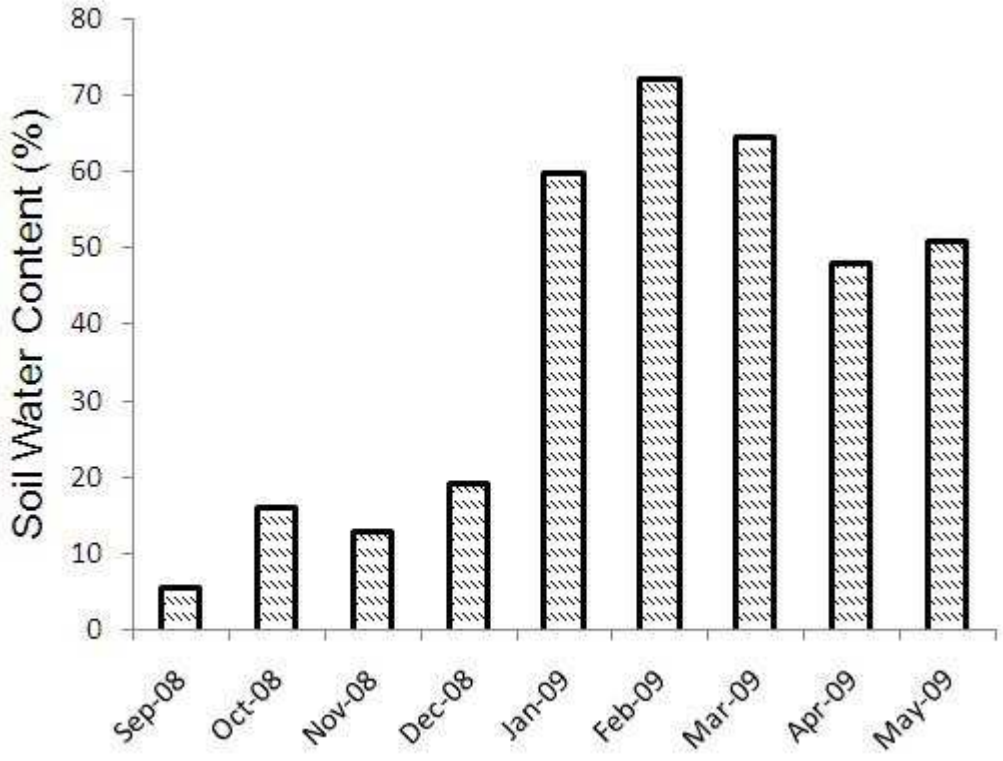

Figure 2: Soil water content measured at Ukulinga during September 2008 to May 2009.

Discussion

The objective of the study was to measure the effects of different planting dates on the growth and yield components of two selected landraces in relation to changes in soil water content during the growing season. The performance of landraces was compared to that of two popular hybrids under field conditions. The first planting was in late August (early planting) before the onset of the rains, with the second planting in late October, set at the onset of the rains (optimum), and the third in January towards the end of the season (late planting).

Planting date was shown to affect emergence of all varieties significantly (Table 2). Contrary to reports that early planting usually results in reduced or poor and unsynchronised emergence due to a lack of soil water in the seedbed at planting (Mwale *et al*., 2003), the highest emergence was recorded in the early planting. Under conditions of low soil water content, Landrace A and Landrace B out-emerged the hybrids. However, the lack of soil water and low average temperatures resulted in all varieties emerging only 35 DAS in the early planting. The minimum temperature for germination in maize is 10℃, below which germination fails to occur (Arnon, 1972). Optimum planting resulted in the lowest emergence while emergence recovered again in the late planting. This was as a result of increased rainfall, soil water content (72%) and warmer temperatures (average temperature of 16℃). Germination and especially emergence is far more rapid and uniform at soil temperatures of 16-18℃ (Arnon, 1972). On average, landraces emerged better compared to hybrids in all three plantings.

Plant height and leaf number are established growth parameters and indices of water stress tolerance. Reduction in leaf number under water deficits is a result of reduced leaf appearance rate and reduced plant height as well as accelerated leaf senescence (Carberry *et al*., 1993a, b; Belaygue et al., 1996; Marcelis *et al*., 1998; Gupta *et al*., 2001; Pic *et al*., 2002). Early planting resulted in the shortest plants with the least number of leaves since it coincided with the driest period. The vegetative stage of the optimum planting coincided with increasing soil water content and temperature, resulting in plants expressing their genetic potential. Plant height and leaf number decreased slightly in the late planting in response to decreasing soil water content and temperature. Aldrich *et al*. (1975) associated late planting with a shortened season; this may have limited plant growth. Over-all, hybrids were taller than landraces, although they had similar leaf number with landraces.

Early planting took the longest time to tassel followed by optimum and late planting, respectively. Early planting has been reported to enjoy a longer growing season when compared to optimum and late planting (Aldrich *et al*., 1975; 1986). Tasseling in the early and optimum planting coincided with increased rainfall and soil water content whilst the late planting coincided with decreasing temperatures, rainfall and soil water content. This pattern was consistent with that suggested by Otegui and Melon (1997). Both hybrids and landraces were similar, with respect to DTT, confirming that landraces were late maturing varieties.

For yield components, planting date had no effect on ear length and mass, kernel rows per ear, grain mass per plant and yield. Planting date however, had an effect on

ear prolificacy; KNE and 100 GM (Table 3). Ear prolificacy is genotype specific and is already determined at the onset of tasseling, together with ear size. Water stress at this point can reduce cob size and potential yield (Heinigre, 2000). Such were the differences observed between hybrids and landraces. Landrace A and Landrace B had the highest number of ears, respectively, compared to SC701 and SR52 in all three planting dates. Ear prolificacy was highest in the optimum and early planting because tasseling coincided with favourable conditions, allowing plants to fully express their genetic potential. Variation in planting date has been shown to influence kernel numbers per ear (Harris, 1984). Contrary to reports by Otegui and Melon (1997), results observed showed that kernel number was highest in the late planting.

Rainfall and soil water content data showed that reproductive stages for both early and optimum planting coincided with the most favourable period in the growing season. In the late planting, the reproductive stage coincided with a progressive decrease in rainfall, soil water content and temperature. The optimum and late planting had shorter growing periods, compared to early planting. Consequently, there was more biomass accumulation (100GM) in the early planting when compared to the other two plantings. Taylor and Blackett (1982) reported that due to a shorter growing season, there may be a tendency for later planted crops to give lighter grains. These results are also consistent with those of Otegui and Melon, (1997). However, planting date had no effect on grain mass per plant and total yield. This is due to gains that were made elsewhere. Although, the optimum and late planting had a shorter growing period, hybrids and landraces were considerably taller with more

leaves. This meant hybrids and landraces' capacity to photosynthesise was compensated for by these gains.

According to Green *et al*. (1985), results of planting dates may vary and can be inconsistent between seasons and sites and that it is not unusual for late planted crops to out-yield the optimum planting. Hybrids had highest yield in the early and late plantings, respectively. Yield of landraces increased with successive planting dates, reaching its highest in the late planting.

Conclusion

Hybrids dominated the landraces in all, but one, aspect – ear prolificacy. Landraces had a greater number of ears per plant compared to hybrids. However, landraces' advantage in ear prolificacy did not translate to other yield components as landraces had smaller ears with fewer rows and kernels compared to hybrids. Ultimately, hybrids achieved higher yields compared to landraces. Landraces increased in most yield components in the optimum and late plantings while the hybrids either decreased slightly or remained consistent. Early planting favoured a longer growing season with increased biomass accumulation and hybrids responded well to this. It also positioned the critical growth stages of maize away from stressful periods and in a sort of "optimum window". Optimum planting experienced a shorter growing period; plants were able to compensate for this effect by increasing their height and leaf number. Late planting experienced the shortest growing period and would be recommended for short season variety hybrids. However, average yields achieved by the landraces in all plantings were higher than the 1.5t/ha attained by most farmers in

dryland farming. They also exhibited a degree of stress tolerance compared to hybrids as yield increased in the late planting. These results warrant further field trials.

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References

(See final reference section, pages 111-142)

CHAPTER 5

CAN HYDRO-PRIMING IMPROVE GERMINATION SPEED, VIGOUR AND EMERGENCE OF MAIZE LANDRACES UNDER WATER STRESS?

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Abstract

Hydro-priming has recently been used to improve establishment in many crops but has not been studied for maize landraces. The aim of this study was to observe whether hydropriming can improve germination speed, vigour and seedling emergence of a local maize landrace under water stress conditions. Two variations of landraces, white (Land A) and dark red (Land B), together with two locally popular hybrids, SC701 and SR52, were either not primed (UP) or primed by soaking in water for 12 hours (P12) and 24 hours (P24), respectively. Seeds were incubated in a germination chamber at 25℃ for 8 days. For seedling emergence, seeds were planted in seedling trays at 25% FC and 75% FC, respectively, in a temperature controlled glasshouse (25℃ day; 15℃ night; 60% RH). Priming did not increase final

germination. Hybrids performed better than landraces when seeds were not primed. Priming landraces for 12 hours and 24 hours reduced mean germination time (MGT) by 9% and 7%, respectively, while priming seeds for 12 hours improved germination velocity index (GVI) by 40%. There was a highly significant interaction ($P<0.001$) between variety and priming for germination traits such as root and shoot lengths and fresh mass. There were no differences ($P>0.05$) in seedling emergence. Priming seeds for 24 hours improved emergence at 25% FC while priming for 12 hours improved emergence at 75% FC. There was a highly significant interaction ($P<0.001$) between priming and field capacity for mean emergence time (MET). Priming seeds for 24 hours reduced MET for all varieties. Priming seeds for 12 hours and 24 hours increased leaf area by 33.8% and 29%, respectively. Hydropriming improved germination speed, reduced MGT and improved emergence and vigour of landraces under water stress.

Keywords: Emergence, germination, hydropriming, landraces, water stress

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Introduction

Good crop establishment is essential for the efficient use of water (Monteith & Elston, 1983) and is a major constraint to crop production in the semi-arid tropics (Itabari *et al*., 1993; Harris *et al*., 1999; Matarira *et al*., 2004). This is particularly true for maize which does not tiller (Finch-Savage *et al*., 2004). Good germination and emergence are important for achieving good crop establishment and maximum possible plant populations in the field, more so under adverse growing conditions. As such, speed of germination and emergence is important for successful establishment (Harris, 1996).

Technology that enhances germination and emergence is thus important in mitigating deleterious effects of poor crop establishment due to drought. Such technology would allow farmers to achieve good crop stands and ultimately good yields. Seed priming is one such technology which has been developed to enhance the germination characteristics of seeds (Foti *et al*., 2008). Its purpose is to partially hydrate the seeds to a point were germination processes are initiated but not completed (Heydecker *et al*., 1973; McDonald, 2000). Primed seeds exhibit rapid germination and emergence under field conditions (Ashraf & Foolad, 2005).

There is a variety of methods that have been used to study the effect of seed priming on germination and growth rate of maize. These include osmo-priming (soaking seeds in osmotic solutions such as polyethylene glycol (PEG)), halo-priming (soaking seeds in salt solutions), hydro-priming (soaking seeds in water), hormonal-priming and matri-priming (Chiu *et al*., 2002; Kao *et al*., 2005; Windauer *et al*., 2007; Ghassemi-Golezani *et al*., 2008). Priming maize seed using PEG or potassium salts

(K_2HPO_4 or KNO_3) accelerated germination in a chilling germinator (10℃) (Basra *et al.,* 1989). Soaking maize seed in 2.5% potassium chloride (KCl) for 16 hours reduced coleoptile and radicule length, while seed soaked in 20 ppm GA_3 for 30 min improved some germination traits (Subedi & Ma, 2005).

Hydro-priming (henceforth referred to as priming) is a simple low-cost method of seed priming that requires no sophisticated equipment and gives results which are easy to see (Foti *et al*., 2008). Nagar *et al.* (1998) observed a significant improvement in field emergence and seedling characteristics after hydro-priming maize for 16 hours. In a series of experiments, Harris *et al*. (1999) showed that hydro-priming markedly improved establishment and early vigour of upland rice, maize and chickpea, and resulted in faster development, earlier flowering and maturity and higher yields. This simple, low-cost, low-risk intervention also had positive impacts on the wider farming system and livelihoods and proved highly popular with farmers (Harris *et al*., 1999, 2001).

The improvement in germination and emergence as a result of priming has been more recently linked to several biochemical changes that occur in the seed. There are reports of increased protein synthesis in response to priming (Capron *et al*., 2000; Gamboa-deBuen *et al*., 2006) as well as evidence of reduced metabolite leakage (Ruan *et al*., 2002; Giri & Schillinger, 2003; Basra *et al*., 2005; Farooq *et al*., 2006). Bailly *et al*. (2000) reported that antioxidant enzymes, including superoxide dismutase (SOD) and catalase (CAT), were expressed when seeds were primed. In addition to

reduced time to 50% emergence and improved final germination, Wahid *et al*. (2008) also observed increased protein synthesis and soluble sugars concentration in response to priming sunflower achenes. They concluded that priming-induced improvements in germination and seedling growth were associated with protein synthesis, membrane repair and greater substrate availability for germination.

Maize landraces are still being grown by subsistence farmers in KwaZulu-Natal, South Africa under a rain-fed system; which according to Rowland (1993) is a risky environment. The risk is related to rainfall amount and distribution (Foti *et al*., 2007) during the time of planting. Farmers normally sow their maize either in late spring, before the onset of rain, or with the first rain. The former crop usually suffers from a dry seedbed, resulting in poor emergence. The latter crop may suffer from rains that usually peter out early. In either case, the result is poor crop establishment leading to poor yields due to reduced plant populations.

The aim of this study was to observe whether priming can be used to improve germination speed and emergence of local maize landraces under water stress conditions. The performance of landraces was compared to two popular hybrids, SC701 and SR52.

Material and Methods

Planting Material

Seed for the landrace was initially donated by local farmers in KwaZulu-Natal, South Africa, and multiplied at the University's Ukulinga Farm in the previous year. The landraces were characterized according to kernel colour, two of which were selected for this study; white (Land A) and dark red (Land B). Two hybrids, SC701 and SR52, were used in this study for the purpose of comparing the landraces' performance.

Seed Priming Procedure

Seeds of landraces and hybrids were soaked in distilled water for 0 hours (Unprimed or control), 12 hours (P12) and 24 hours (P24), respectively. After soaking, the seeds were surface dried.

Laboratory Germination

Three replicates of 25 seeds from each variety and priming treatment combination were germinated between double layered, moistened paper towels (ISTA, 2003). The paper towels were rolled, put into zip-lock bags and incubated in a germination chamber at 25℃ (AOSA, 1992) for 8 days. Radicule p rotrusion was the criterion of germination. Observations for final germination percentage, based on normal seedlings, were made according to AOSA (1992) guidelines. Root and shoot length (mm), root:shoot ratio, fresh and dry mass (g) were measured.

Mean time to germination (MGT) was calculated according to the formulae by Ellis and Roberts (1981):

$$MGT = \frac{\sum Dn}{\sum n}$$

Where:

MGT= mean germination time,

n= the number of seed which were germinated on day D, and

D= number of days counted from the beginning of germination.

Germination speed was calculated based on Maguire's (1962) formulae:

$$GVI = G_1/N_1 + G_2/N_2 + \ldots + G_n/N_n$$

Where:

GVI = germination velocity index

G_1, $G_2 \ldots G_n$ = number of germinated seeds in first, second… last count.

N_1, $N_2 \ldots N_n$ = number of sowing days at the first, second… last count.

Seedling Emergence

Three replicates of 10 seeds from each variety and priming treatment combination were planted in seedling trays using pine bark as growing media at 25% and 75% field capacity (FC), respectively, over a period of 22 days in a controlled environment (25℃ day; 15℃ night; 60% RH) glasshouse. The tray s were weighed and watered at two-day intervals to maintain field capacities. Data collected included daily emergence for 14 days, leaf area (cm^2), root and shoot lengths and root and shoot mass (fresh and dry).

Mean time to emergence was calculated using the formulae by Bewley and Black (1994):

$$\mathrm{MET} = \frac{\sum(fx)}{\sum f}$$

Where MET= mean emergence time,

f= number of newly germinating seeds at a given time (day), and

x= number of days from date of sowing.

Statistical Analysis

Data collected was analysed using GenStat® Version 11 statistical package. Means were separated using LSD $_{(P = 0.05)}$.

Results

Laboratory Germination

Priming had a highly significant effect ($P<0.001$) on final germination. Results for final germination showed there was a significant interaction ($P<0.05$) between priming and variety (Table 1). With the exception of Landrace B, priming did not increase final germination in the other three varieties. Maximum germination (100% for Landrace A and 98.67% for both hybrid varieties) was achieved in the unprimed treatment. For both priming treatments (P12 and P24), final germination fell by an average 8% in the hybrids compared to 4% in landraces. Landrace B attained maximum germination (98.67%) when seeds were primed for 24 hours (P24).

Table 1: Germination attributes of landraces (Land A and Land B) and hybrids (SC701 and SR52) for unprimed (UP), 12 hours (P12) and 24 hours (P24) seeds.

	Variety	Germination	MGT (days)	GVI	Root length (mm)	Shoot length (mm)	Root:Shoot	Fresh mass (g)	Dry Mass (g)
Unprimed	Land A	100a	4.7ab	32.99e	113d	89.5g	1.265abc	1.402c	0.314c
	Land B	97.33abc	4.7ab	34.63de	170.2ab	139.5b	1.227abcd	1.805a	0.304c
	SC701	98.67ab	4.767a	32.79e	135.5cd	102.8fg	1.345ab	1.498bc	0.242d
	SR52	98.67ab	4.5bc	38.46cd	132cd	106f	1.252abc	1.558bc	0.379a
mean		**98.67**^{a}	**4.667**^{a}	**34.72**^{b}	**137.7**^{a}	**109.5**^{b}	**1.272**^{a}	**1.566**^{b}	**0.3097**^{b}
P12	Land A	93.33bc	4.3de	46.84a	114.5cd	163.5a	0.721e	1.895a	0.323bc
	Land B	92c	4.233e	48.35a	109.4d	111.4ef	0.983cde	1.601b	0.298c
	SC701	94.67abc	4.367d	44.43ab	191.7a	133.9bc	1.444a	1.934a	0.373ab
	SR52	86.67d	4.4cd	39.85bc	122.7cd	128.4bcd	0.974de	1.586bc	0.408a
mean		**91.67**^{c}	**4.325**^{b}	**44.87**^{a}	**134.6**^{a}	**134.3**^{a}	**1.03**^{b}	**1.754**^{a}	**0.3503**^{a}
P24	Land A	93.33bc	4.367d	40.17bc	123cd	123.8cde	1.012cd	1.599bc	0.314c
	Land B	98.67ab	4.3de	49.12a	132.3cd	129.4bc	1.053cd	1.454bc	0.297cd
	SC701	97.33abc	4.3de	48.43a	147.7bc	135.8bc	1.09bcd	1.545bc	0.276cd
	SR52	82.67d	4.467cd	34.6de	129.3cd	113def	1.147bcd	1.489bc	0.4a
mean		**93**^{b}	**4.358**^{b}	**43.08**^{a}	**133.1**^{a}	**125.5**^{a}	**1.076**^{b}	**1.522**^{b}	**0.3217**^{b}
LSD (P= 0.05) Variety x Priming		6.422	0.1206	5.371	33.47	15.42	0.2847	0.1988	0.05503
LSD (P= 0.05) Priming		3.211	0.0603	2.685	16.74	7.71	0.1424	0.0994	0.02751

*Note: MGT = mean germination time; GVI = germination velocity index (germination speed). Numbers with different letters in the same column differs significantly at LSD $_{(P=0.05)}$.

Priming had a significant effect (P<0.001) on mean germination time (MGT), reducing it for all varieties. There was a highly significant interaction (P<0.001) between variety and priming in MGT (Table 1). Hybrids germinated faster than landraces when seeds were not primed. The effect of priming on MGT was more pronounced for landraces than hybrids. Priming landraces for 12 and 24 hours reduced MGT by 9% and 7%, respectively, compared to a reduction of 5% for hybrids in both cases.

In addition, significantly increased germination velocity index (GVI) in all varieties. There was a highly significant interaction (P<0.001) between variety and priming with respect to GVI (Table 1). Hybrids germinated 5% faster than landraces when seeds were not primed. However, when seeds were primed for 12 and 24 hours, landraces germinated 11% and 7% faster than hybrids, respectively. Over-all, priming seeds for 12 hours had the greatest effect on landraces, improving the GVI by 40% when compared to unprimed seeds.

Furthermore, there was a highly significant interaction (P<0.001) between variety and priming for germination vigour traits such as root and shoot lengths and fresh mass (Table 1). Root length for landraces declined by 20% (P12) and 9% (P24) as compared to the maximum root length reached when seeds were not primed. Landrace B, in particular was negatively affected by priming. Root length of hybrids increased in response to priming. Roots of hybrids were 28% and 7% longer than landraces when seeds were primed for 12 and 24 hours, respectively. Priming increased shoot length for all varieties. Seeds of landraces, primed for 12 and 24hours, respectively, had about 22% and 10% longer shoots than the unprimed

seeds. Primed seeds of hybrids were 25% (P12) and 19% (P24) longer than unprimed seeds. Overall, landraces responded better than hybrids to priming with regard to shoot length by 7% (P12) and 1.7% (P24). Lastly, priming had a significant effect ($P<0.05$) on dry mass. Landraces had a marginal increase (<1%) when seeds were primed for 12 hours. Hybrids showed an increase in dry mass of 25% and 8% when seeds were primed for 12 hours and 24 hours, respectively.

Seedling Emergence

There were no differences ($P>0.05$) in seedling emergence (Fig 1) with respect to variety, priming and field capacity. There was also no significant interaction ($P>0.05$) between the three treatment factors. SR52 was adversely affected when seeds were primed for 24hours. Emergence improved under water stress when seeds were primed for 24hours. There was no significant ($P>0.05$) three way interaction with respect to mean emergence time (MET) (Fig 2). However, there was a highly significant interaction ($P<0.001$) between priming and field capacity (Fig 2). MET was reduced when seeds were primed for 24 hours in all varieties (Fig 2). Priming seeds for 12 hours improved emergence under optimum conditions (75% FC) and not under water stress (25% FC).

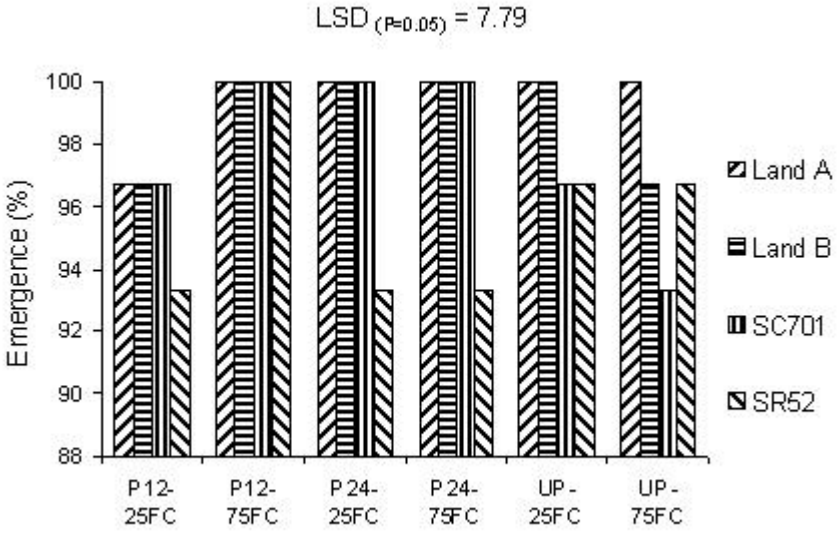


Figure 1: Seedling emergence for landraces (Land A and Land B) and hybrids (SC701 and SR52) grown at 25% FC and 75% FC after seeds were either not primed (UP) or primed for 12 (P12) and 24 (P24) hours.

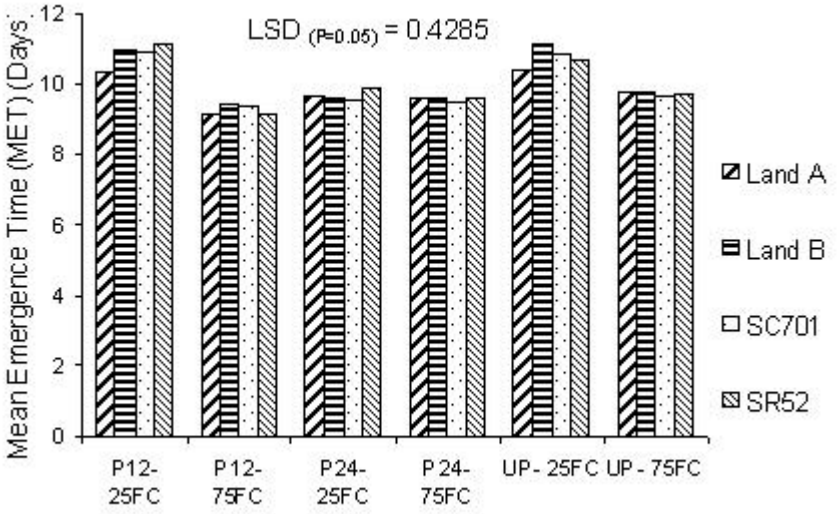


Figure 2: Mean emergence time (MET) for landraces (Land A and Land B) and hybrids (SC701 and SR52) grown at 25% FC and 75% FC after seeds were either not primed (UP) or primed for 12 (P12) and 24 (P24) hours.

There was no significant three way interaction (P>0.05) between variety, priming and field capacity for all seedling characteristics (Table 2). With respect to root length, priming and field capacity both had significant effects (P<0.05) while the interaction was also significant (P<0.05) (Table 2). Under water stress conditions (25% FC), root length increased by 4% (P24) and 16% (P12) in response to priming. In particular, landraces increased root length under water stress by 4% (P24) and 21% (P12). Although the interaction between priming and field capacity had no effect (P>0.05) on shoot length (Table 2), priming, on its own, had a highly significant effect (P<0.001) on shoot length. There were no differences in root and shoot dry mass (Table 2).

Leaf area development showed no significant three way interaction (P>0.05) between variety, priming and field capacity (Table 2). Field capacity had a highly significant effect (P<0.001) on leaf area (Table 2), reducing it by about 23% under water stress. Nonetheless, priming had a significant effect (P<0.001) on leaf area, leaf area increased by 33.8% and 29% in response to priming seeds for 12 hours and 24 hours. Leaf area of landraces increased under water stress (25% FC) by 34% (P12) and 6.5% (P24) while leaf area of hybrids increased by 48.5% (P12) and 47% (P24), respectively.

Table 2: Seedling characteristics of landraces (Land A and Land B) and hybrids (SC701 and SR52) at 25% and 75% field capacity, respectively.

Treatment		Variety	Root Length (mm)	Shoot length (mm)	Root: Shoot	Root DM (g)	Shoot DM (g)	Leaf area (cm^2)
Unprimed	25 FC	Land A	55.33^{cde}	204.3^{d}	0.276^{bcd}	0.2733^{bcdefg}	0.1367^{abcde}	36.2^{def}
		Land B	56^{cde}	185^{d}	0.304^{abc}	0.2167^{fgh}	0.1133^{bcde}	35.8^{def}
		SC701	65^{abcd}	187^{d}	0.4061^{a}	0.3133^{abcde}	0.0967^{cde}	35.8^{def}
		SR52	45^{e}	177.3^{d}	0.2627^{bcd}	0.3367^{abcd}	0.0767^{e}	29.2^{f}
P12	25 FC	Land A	66.67^{abc}	261.7^{abcd}	0.2547^{bcd}	0.1767^{h}	0.1533^{abcd}	51.9^{bcde}
		Land B	68.33^{ab}	224.7^{cd}	0.3033^{abc}	0.21^{fgh}	0.14^{abcde}	45.8^{bcdef}
		SC701	62.33^{bcd}	259.3^{abcd}	0.2416^{bcd}	0.3967^{a}	0.15^{abcd}	49.2^{bcdef}
		SR52	60.67^{bcd}	250.7^{abcd}	0.243^{bcd}	0.3467^{abc}	0.14^{abcde}	47.3^{bcdef}
P24	25 FC	Land A	53.33^{de}	234.3^{bcd}	0.2288^{bcd}	0.2^{gh}	0.1267^{bcde}	43.3^{cdef}
		Land B	62.67^{bcd}	198.7^{d}	0.3204^{ab}	0.2567^{cdefgh}	0.12^{bcde}	33.4^{ef}
		SC701	57.33^{bcd}	294.7^{a}	0.1942^{d}	0.27^{bcdefgh}	0.1467^{abcde}	61^{abc}
		SR52	58.33^{bcd}	206.3^{d}	0.289^{abcd}	0.36^{ab}	0.0833^{de}	34.6^{ef}
Unprimed	75 FC	Land A	58.67^{bcd}	215.7^{d}	0.2721^{bcd}	0.21^{fgh}	0.1333^{abcde}	44.3^{cdef}
		Land B	63b^{cd}	226.7^{cd}	0.2783^{bcd}	0.1967^{gh}	0.1267^{bcde}	37.5^{def}
		SC701	62.67^{bcd}	284.7^{ab}	0.2243^{bcd}	0.29^{bcdefgh}	0.1367^{abcde}	59.5^{abc}
		SR52	53.33^{cde}	217^{cd}	0.2459^{bcd}	0.3267^{abcd}	0.09^{de}	41.7^{cdef}
P12	75 FC	Land A	65^{abcd}	296.7^{a}	0.2233^{bcd}	0.2233^{efgh}	0.18^{ab}	59.9^{abc}
		Land B	57.67^{bcd}	199^{d}	0.2941^{abcd}	0.2467^{defgh}	0.1133^{bcde}	36.1^{def}
		SC701	63.33^{bcd}	250.7^{abcd}	0.2555^{bcd}	0.3033^{abcdef}	0.1633^{abc}	61.3^{abc}
		SR52	60.33^{bcd}	300^{a}	0.203^{cd}	0.2933^{bcdefg}	0.2033^{a}	76.8^{a}
P24	75 FC	Land A	65.33^{bcd}	249.7^{abcd}	0.2834^{bcd}	0.2833^{bcdefg}	0.1533^{abcd}	53.4^{bcde}
		Land B	61.67^{bcd}	258.7^{abcd}	0.239^{bcd}	0.23^{efgh}	0.18^{ab}	55.8^{bcd}
		SC701	67^{abc}	300.7^{a}	0.2235^{bcd}	0.2767^{bcdefg}	0.1733^{ab}	66.3^{ab}
		SR52	75.67^{a}	273.3^{abc}	0.2773^{bcd}	0.2667^{bcdefgh}	0.1733^{ab}	65.4^{ab}
$LSD_{(P=0.05)}$Var*Priming*FC			12.159	57.24	0.10798	0.09336	0.07179	20.68

*Note: FC= Field Capacity; DM= Dry Mass. Numbers with different letters in the same column differ significantly at $LSD_{(P=0.05)}$

Discussion

Priming of seed has been effectively used to enhance the vigour and emergence of seedlings under both optimal (Demir & van de Venter, 1999; Farooq *et al*., 2006) and sub-optimal conditions (Wahid & Shabbir, 2005; Wahid *et al*., 2007). The objective of this study was to determine whether or not hydropriming can be used to improve vigour, with respect to germination attributes and seedling emergence under water stress, in landraces and thus improve crop establishment.

Priming had a negative impact on final germination; final germination declined by an average 8% in hybrids and 4% in landraces for both priming periods. Rapid uptake of water during priming may have caused imbibition injury, resulting in failure of seeds to germinate. There are similar instances in literature reporting imbibitional injury in seeds, including maize (Pollock, 1969; Cal & Obendorf, 1972; Harrison, 1973; Powell & Mathews, 1978; reviewed by Taylor *et al*., 1992; Bedi & Basra, 1993). Although most of these reports show imbibitional damage at low temperatures, imbibitional damage at higher temperatures, although less severe, can also reduce germination (Finch-Savage *et al*., 2004).

Priming significantly ($P<0.001$) improved germination speed and reduced MGT. Primed seeds germinated faster and more uniformly than unprimed seeds. Although priming reduced root lengths in landraces, it significantly ($P<0.001$) increased shoot lengths, fresh mass and dry mass; suggesting that a greater part of seed reserves were channelled to the shoots which is crucial for early establishment and photosynthesis. Priming improved seed vigour overall, with landraces performing well

when seeds were primed for 12 hours. These results are similar to others reported in literature (Harris *et al*., 1999)

Successful crop establishment determines plant density, uniformity and management options (Cheng & Bradford, 1999) and depends not only on the rapid and uniform germination of the seed, but also on the capacity of the seed to emerge under water stress (Fischer & Turner, 1978). Alleviating the deleterious effect of water stress at this stage can increase chances for attaining a good crop (Ashraf & Rauf, 2001).

Priming increased seedling emergence under both optimum and water stress conditions. Priming for 12 hours improved emergence of the landraces at 75% FC while priming for 24 hours resulted in better emergence for all varieties at 25% FC. Priming for 24 hours resulted in reduced MET under water stress. Priming also resulted in increased root and shoot lengths as well as increased leaf area in landraces. Therefore, priming resulted in improved crop establishment and healthier seedlings. Similar results have been reported in numerous other crops. Ghassemi-Golezani *et al*. (2008) reported that hydro-priming improved seedling emergence rate and percent in lentil; Harris *et al*. (1999) reported enhanced seedling establishment and early vigour of upland rice, maize and chickpea after hydro-priming; Kibite and Harker (1991) reported that seed hydration improved uniformity of seedling emergence of wheat, barley and oat seeds.

Conclusion

Good crop establishment is a prerequisite for successful crop production especially under water stress conditions. Priming had variable effects on germination and emergence of landraces. Seeds responded better to priming for 12 hours when conditions were optimum while priming for 24 hours improved emergence, reduced MET and improved seedling characteristics under water stress. Hydro-priming can be used to improve germination speed, vigour and seedling emergence of landraces under water stress.

References

(See final reference section, pages 111-142)

GENERAL DISCUSSION

Maize landraces have been around since the introduction of maize into southern Africa in the 16th century. Landraces have, through the years, survived under some of the most adverse of growing conditions. Landraces are credited for being the progenitors of conventional modern day hybrids (Zeven, 1998). However, due to increasing drought, research had over the past focussed on developing high yielding, drought tolerant varieties.

To date, landraces have received limited research attention and little is known on its water use and agronomic requirements. The overall aim of this thesis was to study the responses of a local maize landrace to water stress under controlled and field conditions. The responses of landraces were compared to two locally popular hybrids, SC701 and SR52.

Despite its popularity, maize is generally not a drought tolerant crop. South Africa, with its erratic rainfall, is however, prone to water scarcity or periods of drought at anytime during the plant's growth. According to Weltzien and Srivastava (1981), a level of sensitivity to water stress exists at all stages of plant growth. In maize it appears that there are several critical stages of sensitivity. Such sensitivity varies and has varying effects on the final yield of the crop. Figure 6.1 shows the holistic approach of the study and the processes by which the study sought to understand the responses of the landraces to water stress at various phenological stages and physiological responses.

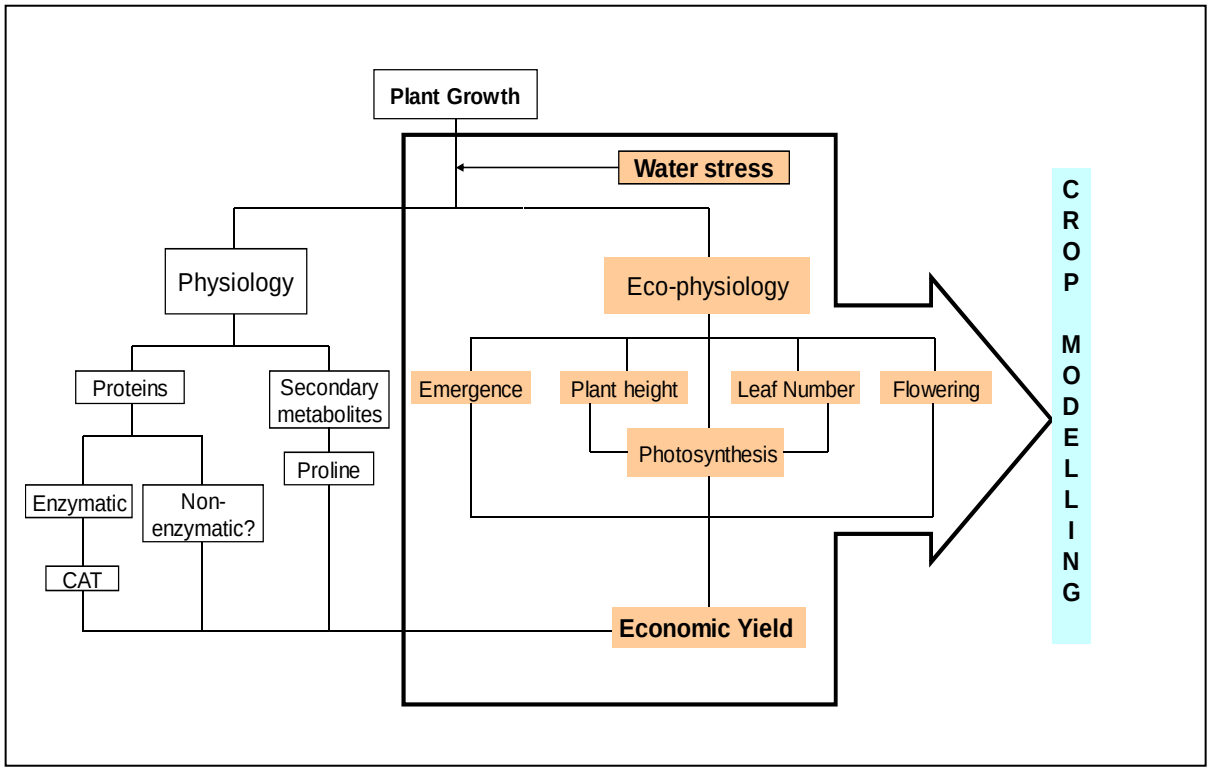


Figure 6.1: Hypothetical (representing activities of the present study and potential future studies) model showing the physiological and morphological aspects of maize growth that are affected by water stress. *Note:**?** represents an area that requires further study.

The first phenological stage occurs at germination and emergence. Edmeades and Bolanos (1997) described a drought tolerant crop at this stage as one which germinates and establishes under dry soil, has a high root:shoot ratio and can actively accumulate solutes in its cells. The first study (Chapter 2) showed that water stress at this stage had serious deleterious effects on plant population. Although the landrace showed a degree of stress tolerance at this stage compared to the hybrids, its emergence was still greatly undermined by the occurrence of water stress at this stage.

Results (Chapter 2) showed that while landraces had the same viability as hybrids, they lacked in certain vigour characteristics. This resulted in them germinating and emerging slower than hybrids under both non-stress and water stress conditions. According to Perry (1978), vigour is important for successful seedling emergence. The study gave birth to the need for improving vigour of the landraces. This led to hydro-priming (Chapter 5) as a low cost alternative to improving vigour characteristics under water stress conditions.

The use of hydro-priming to improve germination, emergence and vigour in crop plants has been successfully used in many other crops; maize, upland rice and chickpea (Harris *et al*., 1999). Hydro-priming landraces for different periods of time resulted in varying effects on germination and vigour traits under water stress. It resulted in 40% faster germination and improved emergence as well as leaf area and other vigour traits under water stress. However, this technique still requires further study to evaluate if the initial positive effects observed on the seedling stage translate into improved crop yield under field conditions.

Recently, there has been evidence to support a link between certain biochemical characteristics and vigour (Randhir & Shetty, 2003). Traditional agronomic methods of seed vigour measurement have included germination percentage, shoot and root length, shoot and root mass. This study (Fig 6.1) explored the accumulation of antioxidants, specifically catalase, and secondary metabolites, specifically proline, in response to water stress (Chapter 2). Results showed that there exists evidence of both catalase and proline accumulation in leaves of landrace maize seedlings

exposed to water stress. Although there is debate on the exact role of proline, it is believed to be involved in osmoregulation. Accumulation of proline at the germination and emergence stage is in line with Bolanos and Edmeades' (1997) description of a drought tolerant crop. Expression of catalase at germination and emergence explained in some way in explaining the level of water stress tolerance exhibited by landraces.

The second stage of sensitivity to water stress exists at the vegetative stage. In maize, this stage covers the period between emergence up to and including tasseling. Effects of water stress at this stage may include reduction in plant height, reduced leaf number and leaf area and ultimately a reduction in photosynthesis (Fig 6.1). Available information relating water stress during the vegetative stage to yield and yield components shows that maize is less sensitive to water stress at this stage than in the later pollination and grain filling stage (Wilson, 1968; Classen & Shaw, 1970; Musik & Dusek, 1980). As a result, most studies have focussed on water stress occurring a few days or weeks before, during or after pollination (Shaw, 1974; Fray, 1982; Coffman, 1998; Lauer, 2003). However, the attainment of maximum leaf area and plant height during the vegetative stage are essential if the plant is going to maximise on its photosynthetic capacity and produce enough assimilate for grain filling.

In a controlled environment study (Chapter 3), water stress was imposed throughout the plants' life cycle, from emergence to maturity. Results showed that water stress had no effect on leaf numbers. A decrease in plant height was observed under water

stress, albeit not significant. Furthermore, photosynthesis, as measured by chlorophyll fluorescence was not affected by water stress; landraces increased photosynthesis under water stress. However, yield components were severely affected by water stress; Landrace A was barren under water stress. This study showed that the effects of water stress were more pronounced on the yield components than during the vegetative stage. These results confirmed similar reports in the literature stating that the vegetative stage is less sensitive to water stress and that photosynthesis in C4 plants is generally desiccation tolerant, up to a certain level (Dhillon *et al*., 1995; Lal & Edwards, 1996; Blum, 1997; Young & Long, 2000). Heinigre (2000) stated that dry weather that starts early and covers several growth periods will have a compounding effect with severe reductions in maize yields. However, these results required further verification under field conditions as controlled experiments are not always reflective of field conditions with numerous variable factors involved.

The effect of planting dates and soil water content on maize yield and yield components under field conditions were studied (Chapter 4). The aim was to not only explore the performance of the landrace under field conditions but moreover to quantify the effects of water stress occurring at different stages of growth on yield components. Of interest was the third sensitive stage of maize, the reproductive stage, which has been described as being the most sensitive to water stress (Doorenbos & Kassam, 1979). Edmeades and Bolanos (1997) described a drought tolerant plant at this stage as being characterised by rapid ear growth at flowering,

relatively short in stature, prolific under well-watered conditions but single-eared and not barren under water stress.

Early planting produced plants that were shorter and with fewer leaves than in subsequent plantings. This was the result of a combination of low soil water content and low temperatures occurring during the vegetative stage. Maximum plant height and leaf number were observed in the optimum and late plantings when temperatures and soil water content had increased.

Landraces improved, with respect to yield and yield components, in the optimum and late plantings, despite attaining its highest biomass accumulation (100 GM) in the early planting. This was possibly due to a longer growing period and favourable conditions around the sensitive period of flowering to maturity. Landraces achieved maximum yield in the late planting, despite the reproductive stages coinciding with a decline in soil water content and temperature. Unfortunately, all three plantings managed to flower when conditions of soil water content were favourable. As such we were unable to quantify the effect of water stress occurring during the reproductive stages under field conditions. Plants avoided such a scenario by either delaying tasseling (early planting) or tasseling early (optimum and late planting). This may be a mechanism of drought avoidance under field conditions.

CONCLUSIONS

Maize landraces still remain an important genetic resource. Landraces emerged slower, were shorter and with fewer leaves, and ultimately yielded less than the hybrids. However, landraces demonstrated a degree of water stress tolerance at the establishment stage, and managed to out-emerge the hybrids under field conditions. There was evidence of catalase expression and proline accumulation at the germination and emergence stage. Under both controlled and field conditions, landraces performed in most instances similar to hybrids during the vegetative stage. Landraces were able to tolerate drought during the vegetative stage and were able to increase photosynthesis under water stress. Water stress severely affected yield of landraces under controlled conditions, and to a lesser extent under field conditions. In both scenarios, landraces yielded considerably less than hybrids. However, yield of landraces was greater than normally attained for dryland maize (1.5t/ha). Superior yields of hybrids may be a result of superior genetic makeup. Landraces were shown to be very prolific, although there was no evidence for yield compensation. Under field conditions, landraces showed a tendency to respond better to optimum and late planting dates than early planting.

References

(See final reference section, pages 111-142)

RECOMMENDATIONS

The following recommendations may be made, based on observations made during the study;

- Hydro-priming seeds for varying periods of time may be used as a low cost technology to enhance emergence and vigour of landraces under both optimum and water stress conditions. However, there is need for further research to see whether these initial benefits contribute to higher yields under water stress.
- Under field conditions, water stress hardly acts alone but in combination with temperature. Therefore, it is imperative to study the effects of both water stress and temperature on emergence, growth and yield of landraces.
- Plants were shown to be less sensitive to water stress at the vegetative stage. Thus, a separate study to observe the effects of water stress occurring at the reproductive stage would add to the knowledge of landraces.
- Lastly, there is need for further research under field conditions. Data collected in this study and future studies may be of use to crop modellers. Crop modelling is an important research and policy making tool. Such a future study would be useful as a tool for policy formulation and identification of future research areas on landraces.

REFERENCES:

ABO-EL-KHEIR, M.S.A. & MEKKI, B.B., 2007. Response of maize single cross-10 to water deficits during silking and grain filling stages. *World J. Agric. Sci.* 3, 269-272.

ACEVEDO, E., HSIAO, T. C. & HENDERSON, D. W., 1971. Immediate and subsequent growth responses of maize leaves to changes in water stress. *Plant Physiol.* 48, 631-636.

AGUILERA, C., STIRLING, C.M. & LONG, S.P., 1999. Genotypic variation within *Zea mays* for susceptibility to and rate of recovery from chill-induced photoinhibition of photosynthesis. *Physiol. Plant*. 106, 429-436.

AHMED, A.G. & MEKKI, B.B., 2005. Yield and yield components of two maize hybrids as influenced by water deficit during different growth stages. *Egypt J. Appl. Sci.* 20, 64-79.

ALDRICH, S.R., SCOTT, W.O. & HOEFT, R.G., 1986. Modern corn production. A&L Publications, Champaign, III.

ALMANSOURI, M., KINET, J.M. & LUTTS, S., 2001. Effect of salt and osmotic stresses on germination in durum wheat (*Triticum durum* Desf.). *Plant Soil* 231, 243-254.

ANDA, A. & PINTER, L., 1994. Sorghum germination and development as influenced by soil temperature and water content. *Agron. J.* 86, 621-624.

ANDREWS, J., 1993. Diffusion of the mesoamerican food complex to southern Europe. *Geographical Review* 83, 194-204.

ANGELOPOULOS, K., DICHIO, B. & XILOYANNIS, C., 1996. Inhibition of photosynthesis in olive trees (*Olea europaea* L) during water stress and re-watering. *J. Exp. Bot*. 47, 1093-1100.

AOSA, 1992. Association of Official Seed Analysts: Seed Evaluation Handbook. Contribution No.35.

ARNON, I., 1972. Crop production in dry regions, Volume II: Systematic treatment of the principal crops, Leonard Hill, London. pp 146-184.

ARORA, A. & MOHAN, J., 2001. Expression of dwarfing genes under nitrogen and moisture stress in wheat (*Triticum* spp.): Dry matter partitioning, root growth and leaf nitrogen. *J. Agron. Crop Sci*. 186, 111-118.

ASADA, K., 1999. The water-water cycle in chloroplast: Scavenging of active oxygen and dissipation of excess photons. *Ann*. *Rev*. *Plant Physiol*. *Plant Mol*. *Biol*. 50, 601-639.

ASHRAF, M. & FOOLAD, M.R., 2005. Pre-sowing seed treatment-a shotgun approach to improve germination growth and crop yield under saline and none-saline conditions. *Advan. Agron*. 88, 223-271.

ASHRAF, M. & RAUF, H., 2001. Inducing salt tolerance in maize (*Zea mays* L.) through seed priming with chloride salts, growth and ion transport at early growth stages. *Acta Physiol. Plant*. 23, 407-414.

ASPINALL, D. & PALEG, L.G., 1981. Proline accumulation: physiological aspects. In: L.G. Paleg and D. Aspinall (Eds.), The physiology and biochemistry of drought resistance in plants. Academic Press, Sydney. pp 215-228.

AUSTIN, R.B., 1989. Maximizing crop production in water-limited environments. In: F.W.G. Baker (Ed.), Drought resistance in cereals. CAB International. pp 13-26.

AZAM-ALI, S., 2009. Fitting underutilized crops within resource-poor environments: Lessons and Approaches. Abstract. *Proceedings of the Symposium on Underutilised Indigenous and Traditional Crops: Agronomy and Water Use.* 18-19 January 2009, Stellenbosch, Western Cape, South Africa.

BAILLY, C., BENAMAR, A., CORBINEAU, F. & COME, D., 2000. Antioxidant systems in sunflower (*Helianthus annus*, L) seeds as affected by priming. *Seed Sci. Res*. 10, 35-42.

BAKER, N.R. & HOLLON, P., 1987. Chlorophyll fluorescence quenching during photoinhibition. In: Kyle, D.L., C.B. Osmond and C.J. Arntzen (Eds.), Photoinhibition. Elsevier Science Publishers B.V., Amsterdam, pp 145-168.

BASRA, A.S., DHILLON, R. & MALIK, C.P., 1989. Influence of seed pre-treatment with plant growth regulators on metabolic alterations of germinating maize embryos under stressing temperature regimes. *Ann. Bot. (London)*. 64, 37-41.

BASRA, S.M.A., FAROOQ, M., TABASSAM, R. & AHMAD, N., 2005. Physiological and biochemical aspects of pre-sowing seed treatments in fine rice (*Oryza sativa* L.). *Seed Sci. Technol*. 33, 623-628.

BASSETTI, P. & WESTGATE, M.E., 1993. Water deficit affects receptivity of maize silks. *Crop Sci*. 33, 279-282.

BASU, R.N., 1995. Seed viability. In: Basra, A.S. (Ed.), Seed Quality: Basic mechanisms and agricultural implications, Food Products Press.

BATES, L.S., WALDEN, R.P. & TEARE, I.D., 1973. Rapid determination of free proline for water stress studies. *Plant and Soil* 39, 205-207.

BAYOUMI, T.Y., MANAL, H. EID & METWALI, E.M., 2008. Application of physiological and biochemical indices as a screening technique for drought tolerance in wheat genotypes. *Afri. J. Biotec.* 7, 2341-2352.

BEADLE, G.W., 1939. Teosinte and the origin of maize. *Journal of Heredity* 30, 245-247.

BEDI, S. & BASRA, A.S., 1993. Chilling injury in germinating seeds: basic mechanisms and agricultural implications. *Seed Sci. Res*. 3, 219–229.

BELAYGUE, C., WERY, J., COWAN, A.A. & TARDIEU, F., 1996. Contribution of leaf expansion, rate of leaf appearance, and stolon branching to growth of plant leaf area under water deficit in white clover. *Crop Sci*. 36, 1240-1246.

BENHIL, J., 2002. Climate, water and agriculture: Impacts on and adaptation of agro-ecological systems in South Africa. A case study of the Republic of South Africa. University of Pretoria, SA.

BEWLEY, J.D. & BLACK, M., 1994. Seeds: Physiology of development and germination, Plenum, New York.

BLUM, A. & SULLIVAN, C.Y., 1986. The comparative drought resistance of landraces of sorghum and millet from dry and humid regions. *Ann*. *Bot*. 57, 846-853.

BLUM, A., 1997. Constitutive traits affecting plant performance under stress. In: Developing drought- and low N-tolerant maize. Eds. Edmeades, G.O., Banziger, M., Mickelson, H.R. and Peña-Valdivia, C.B. Proceedings of a Symposium, March 25-29, 1996. CIMMYT, El Batān, Mexico, DF: CIMMYT.

BOLAÑOS, J. & EDMEADES, G.O., 1993. Eight cycles of selection for drought tolerance in lowland tropical maize. II. Response in reproductive behaviour. *Field Crops Res*. 31, 253-268.

BOLANOS, J. & EDMEADES, G.O., 1996. The importance of the anthesis-silking interval in breeding for drought tolerance in tropical maize. *Field Crops Res*. 48, 65-80.

BOLHAR-NORDENKAMPF, H.R., LONG, S.P., BAKER, N.R., OQUIST, G., SCHREIBER, U. & LECHNER, E.G., 1989. Chlorophyll fluorescence as a probe of the photosynthetic competence of leaves in the field: A review of current instrumentation. *Functional Ecology* 3, 497-514.

BOWLER, C., VAN MONTAGU, M. & INZE, D., 1992. Superoxide dismutase and stress tolerance. *Ann. Rev. Plant Physiol. Plant Mol. Biol*. 43, 83-116.

BOYER, J.S., 1992. Mechanisms for obtaining soil water use efficiency and drought resistance. In: Stalker, H.T. and Murphy, J.P. (Eds.), Plant breeding in the 1990s. CAB International, Wallingford, UK. pp 539.

BRACCINI, A.L., RUIZ, H.A., BRACCINI, M.C.L. & REIS, M.S., 1996. Germinação e vigor de sementes de soja sob estresse hídrico induzidos por soluções de cloreto sódio, manitol e polietleno glycol. *Revista Brasileira de Sementes* 18, 10-16.

BRADFORD, M.M., 1976. A rapid and sensitive method for the quantification quantities of protein utilizing the principle of protein dye binding. *Anal. Biochem.* 72, 248-254.

BRAR, G.S., KAR, S. & SINGH, N.T., 1990. Photosynthetic response of wheat to soil water deficits in the tropics. *J. Agron. Crop Sci*. 164, 343-348.

BRAY, E.A., 1993. Molecular responses to water deficit. *Plant Physiol*. 103, 1035-1040.

BURTT-DAVY, J., 1914. Maize: Its history, cultivation, handling and uses. Longmans, Green and Co.

CAL, J.P. & OBENDORF, R.L., 1972. Imbibitional chilling injury in *Zea mays*, L. altered by initial kernel moisture and maternal parent. *Crop Sci*. 12, 369–373.

CAMPOS, H., COOPER, M., HABBEN, J.E., EDMEADES, G.O. & SCHUSSLER, J.R., 2004. Improving drought tolerance in maize: a view from industry. *Field Crops Res*. 90:19-34.

CAPRON, I., CORBINEAU, F., DACHER, F., JOB, C., COME, D. & JOB, D., 2000. Sugarbeet seed priming: effects of priming conditions on germination, solubilisation of 11-S globulin and accumulation of LEA proteins. *Seed Sci. Res*. 10, 243-254.

CARBERRY, P.S., MUCHOW, R.C. & HAMMER, G.L., 1993a. Modelling genotypic and environmental control of leaf area dynamics in grain sorghum. II. Individual leaf level. *Field Crops Res*. 33, 311-328.

CARBERRY, P.S., MUCHOW, R.C. & HAMMER, G.L., 1993b. Modelling genotypic and environmental control of leaf area dynamics in grain sorghum. III. Senescence and prediction of green leaf area. *Field Crops Res*. 33, 329-351.

CÁRCOVA, J., URIBELLAEA, M., BORRÁIS, L., OTEGUI, M.E. & WESTGATE, M.E., 2000. Synchronous pollination within and between ears improves kernel set in maize. *Crop Sci*. 40, 1056-1061.

CARTER, D.C., HARRIS, D., YOUNGQUIST, J.B. & PERSAUD, N., 1992. Soil properties, crop water use and cereal yields in Botswana after additions of mulch and manure. *Field Crops Res*. 30, 97-109.

CARVALHO, N.M. & NAKAGAWA, J., 1980. Sementes: Ciência, tecnologia e produção. *Campinas: Fundação Cargil*. pp 100-111.

CASSMAN, K.G., 1999. Ecological intensification of cereal production systems: yield potential, soil quality and precision agriculture. *Proc. Nati. Acad. Sci. USA*. 96, 5952-5959.

CHARTZOULAKIS, K., NOITSAKIS, B. & THERIOS, I., 1993. Photosynthesis, plant growth and carbon allocation in kiwi cv Hayward, as influenced by water deficits. *Acta Hort*. 335, 227-234.

CHAVES, M.M., PEREIRA, J.S., MAROCO, J., RODRIGUES, M.L., RICARDO, C.P.P., OSORIO, M.L., CARVALHO, I., FARIA, T. & PINHEIRO, C., 2002. How plants cope with water stress in the field. Photosynthesis and growth. *Ann*. *Bot*. 89, 907-916.

CHEN, G. & ASADA, K., 1989. Ascorbate peroxidase in tea leaves: occurrence of two isozymes and the differences in their enzymatic and molecular properties. *Plant Cell Physiol*. 30, 987–998.

CHEN, R.D. & TABAEIZADEH, Z., 1992. Alteration of gene expression in tomato plants (*Lycopersicon esculantum*) by drought and salt stress. *Genome* 35, 385-391.

CHENG, Y., WENG, J. & JOSH, C.P., 1993. Dehydration stress-induced changes in translatable RNAs in sorghum. *Crop Sci*. 33, 1397-1400.

CHENG, Z. & BRADFORD, K. J., 1999. Hydrothermal time analysis of tomato seed germination responses to priming treatments. *J. Exp. Bot*. 33, 89-99.

CHIU, K.Y., CHEN, C.L. & SUNG, J.M., 2002. Effect of priming temperature and storability of primed *sh-2* sweet corn seed*. Crop Sci*. 42, 1996-2003.

CLAASEN, M.M. & SHAW, R.H., 1970. Water deficit effects on grain. II. Grain components. *Agron. J*. 62, 652-655.

CLOSE, T.J. & CHANDLER, P.M., 1990. Cereal dehydrins: Serology, gene mapping and potential functional roles. *Aust*. *J*. *Plant Physiol*. 17, 333-344.

CLOSE, T.J., 1996. Dehydrins: Emergence of a biochemical role of a family of plant dehydration proteins. *Plant Physiol*. 97, 795-803.

COFFMAN, C., 1998. Critical growth stages of corn. Texas Agricultural Extension Service, Texas. Available from: http://lubbock.tamu.edu/corn/pdf/criticalgrowth.pdf (Accessed 16 June 2009)

COMIC, G. & BRIANTAIS, J.M., 1991. Partitioning of photosynthetic electron flow between CO_2 and O_2 reduction in a C3 leaf (*Phaseolus vulgaris* L.) at different CO_2 concentrations and during drought stress. *Planta* 183, 178-184.

COOLBEAR, P. & HILL, M.J., 1988. Seed quality control. In: S.J. Banta (Ed.), Rice seed health, Manila, Philippines: International Rice Research Institute. pp 331-342.

CRAFTS-BRANDNER, S.J. & SALVUCCI, M.E., 2002. Sensitivity of photosynthesis in a C4 plant, maize, to heat stress. *Plant Physiol*. 129, 1773-1780.

DELACHIAVE, M.E.A. & PINHO, S.Z., 2003. Germination of *Senna Occidentalis* Link: Seed at different osmotic potential levels. *Brazilian Arch*. *Biol*. *Tech*. 46, 163-166.

DELAUNEY, A.J. & VERMA, D.P.S., 1993. Proline biosynthesis and osmoregulation in plants. *Plant J*. 4, 215-223.

DELFINE, S., ALVINO, A., LORETO, F., CENTRITTO, M. & SANTARELLI, G., 2000. Effects of water stress on the yield and photosynthesis of field grown sweet pepper (*Capsicum annuum* L.). *Acta Hort*. 537, 223-229.

DELFINE, S., LORETO, F. & ALVINO, A., 2001. Drought-stress effects on physiology, growth and biomass production of rainfed and irrigated bell pepper plants in the Mediterranean region. *J*. *American Soc*. *Hort*. *Sci*. 126, 297-304.

DEMIR, I. & VAN DE VENTER, M.A., 1999. The effect of priming treatment on the performance of water melon (C*itrullus lanatus*) seeds under temperature and osmotic stress. *Seed Sci. Technol*. 27, 871-875.

DEMMING, B. & BJORKMAN, O., 1987. Comparison of the effect of excessive light on chlorophyll fluorescence (77k) and photon yield of O_2 evolutions in leaves of higher plants. *Planta* 171, 171-184.

DEREK, B. & EICHER, C.K., 1997. Africa's Emerging Maize Revolution. Boulder, Colo: Lynne Rienner.

DE-RONDE, J.A., MESCHT, V.D. & STEYN, H.S.F., 2000. Proline accumulation in response to drought and heat stress in cotton. *Afri*. *Crop Sci*. *J*. 8, 85-91.

DHILLON, R.S., THIND, H.S., SASEENA, U.K., SHARMA, R.K. & MALHI, N.S., 1995. Tolerance to excess water stress and its association with other traits in maize. *Crop Improvement* 22, 22-28.

DHINDSA, R.S. & MATOWE, W., 1981. Drought tolerance in two mosses: Correlated with enzymatic defense against lipid peroxidation. *J. Exp. Bot*. 32, 79-91.

DIONISIO-SENSE, M.L. & TOBITA, S., 1998. Antioxidant responses of rice seedlings to salinity stress. *Plant Sci.*135, 1-9.

DONATELLI, M., HAMMER, G.L. & VANDERLIP, R.L., 1992. Genotype and water limitation on effects on phenology, growth, and transpiration efficiency in grain sorghum. *Crop Sci*. 32, 781-786.

DONEEN, L.D. & MACGILLIVRAY, J.H., 1943. Germination (emergence) of vegetable seed as affected by different soil moisture conditions. *Plant Physiol.* 18, 524-529.

DOORENBOS, J. & KASSAM, A.K., 1979. Yield response to water. Irrigation and drainage Paper 33. FAO, United Nations, Rome. pp 176

DORNBOS, D.L., JR., 1995. Seed vigour. In: Basra, A.S. (Ed.), Seed Quality: basic mechanisms and agricultural implications, Food Products Press.

Du TOIT, A.S., PRINSLOO, M.A., DURAND, W. & KIKER, G., 2002. Vulnerability of maize production to climate change and adaptation in South Africa. Combined Congress: South African Society of Crop Production and South African Society of Horticultural Science, Pietermaritzburg, SA.

DURÃES, F.O.M., GAMA, E.E.G., MAGALHÃES, P.C., MARRIEL, I.E., CASELA, C.R., OLIVIERA, A.C., LUCHIARI JUNIOR, A. & SHANAHAN, J.F., 2001. The usefulness of chlorophyll fluorescence in screening for disease resistance, water stress tolerance, aluminium toxicity tolerance and N use efficiency in maize. Seventh Eastern and Southern Africa Regional Maize Conference. pp 356-360.

DURÃES, F.O.M., MAGALHÃES, P.C., FERRER, J.L.R. & MACHADO, R.A.F., 2000a. Adatação de Milho ás Condições de Seca: 2. Florescimento e Maturidade Fisiológica de Sementes de Linhagens Contrastantes para o Parâmetro Fenotípico IFMF. In: CONGRESSO NACIONAL DE MILHO E SORGO, 23, Uberlândia, 2000. Resumos. Uberlândia, MG. ABMS; CNPMS.

DWYER, L.M., STEWART, D.W. & TOLLENAAR, M., 1992. Analysis of maize leaf photosynthesis under drought stress. *Can. J. Plant Sci.* 72, 477-481.

EARL, H.J. & DAVIS, R.F., 2003. Effect of drought stress on leaf and whole canopy radiation use efficiency and yield of maize. *Agron. J.* 95, 688-696.

EARL, H.J. & TOLLENAR, M., 1998. Relationship between thylakoid electron transport and photosynthetic CO_2 uptake in leaves of three maize (*Zea maize* L.) hybrids. *Photosynth. Res*. 58, 245-257.

EDMEADES, G.O. & BOLANOS, J., 1997. Value of secondary traits in selecting for drought tolerance in tropical maize. In: Developing drought- and low N-tolerant maize. Eds. Edmeades, G.O., Banziger, M., Mickelson, H.R. and Peña-Valdivia, C.B. Proceedings of a Symposium, March 25-29, 1996. CIMMYT, El Batān, Mexico, DF: CIMMYT.

EDWARDS, G.E. & BAKER, N.R., 1993. Can CO_2 assimilation in maize leaves be predicted accurately from chlorophyll fluorescence analysis? *Photosynth. Res*. 37, 89-102.

EL MIDAOUI, M., SERIEYS, H., GRIVEAU, Y., BENBELLA, M., TALOUZTE, A., BERVILLE, A. & KAAN, F., 2003. Effects of osmotic water stress on root and shoot morphology and seed yield in sunflower (*Helianthus annus* L.) genotypes bred for Morocco or issued from introgression with *H. argophyllus* T&G and *H. deblis*. *Nutt*. *Helia* 26, 1-16.

ELLIS, R.A. & ROBERTS, E.H., 1981. The quantification of ageing and survival in orthodox seeds. *Seed Sci. Technol.* 9, 373-409.

EPHRATH, J.E. & HESKETH, J.D., 1991. The effects of drought stress on leaf elongation, photosynthetic and transpiration rates in maize (*Zea mays* L.) leaves. *Photosynthetica* 29, 447-454.

EPRON, D., DREYER, E. & BRÉDA, N., 1992. Photosynthesis of oak trees [(*Quercus petraea* (Matt) Liebl.)] during drought stress under field conditions: diurnal course of net CO_2 assimilation and photochemical efficiency of photosystem II. *Plant Cell and Environment* 15, 809-820.

FAROOQ, M., BASRA, S.M.A. & WAHID, A., 2006. Priming of field-sown rice seed enhances germination, seedling established, allometry and yield. *Plant Growth Regul.* 49, 285-294.

FAROOQ, M., BASRA, S.M.A., KHALID, M., TABASSUM, R. & MAHMOOD, T., 2006. Nutrient homeostasis, metabolism of reserves and seedling vigour as affected by seed priming in coarse rice. *Can. J. Bot*. 84, 1196-1202.

FARRE, I., VAN OIJEN, M., LEFFELAAR, P.A. & FACI, J.M., 2000. Analysis of maize growth for different irrigation strategies in north-eastern Spain. *Euro. J. Agron*. 12, 225-238.

FERNANDEZ, R.J., WANG, M. & REYNOLDS, J.F., 2002. Do morphological changes mediate plant responses to water stress? A steady-state experiment with two C4 grasses. *New Phytologist* 155, 79-88.

FINCH-SAVAGE, W.E., 1995. Influence of seed quality on crop establishment, growth and yield. In: Basra, A.S. (Ed.), Seed Quality: Basic mechanisms and agricultural implications, Food Products Press.

FINCH-SAVAGE, W.E., DENT, K.C. & CLARK L.J., 2004. Soak conditions and temperature following sowing influence the response of maize (*Zea mays* L.) seeds to on-farm priming (pre-sowing seed soak). *Field Crops Res.* 90, 361-374.

FISCHER, R.A. & TURNER., 1978. Plant productivity in the arid and semi-arid zones. *Ann. Rev. Plant Physiol.* 29, 277-317.

FOTI, R., ABURENI, K., TIGERE, A., GOTOSA, J. & GERE, J., 2008. The efficacy of different seed priming osmotica on the establishment of maize (*Zea mays* L.) caryopses. *J. Arid Environ*. 72, 1127-1130.

FREY, N.M., 1982. Dry matter accumulation in kernels of maize. *Crop Sci*. 21, 118-122.

GAMBOA-deBUEN, A., CRUZ-ORTEGA, R., MARTINEZ-BARAJAS, E., SANCEZ-CORONADO, M.E. & OROZCO-SEGOVIA, A., 2006. Natural priming as an important metabolic event in the life history of *Wigandia urens* (Hydrophillaceae) seeds. *Physiol. Plant*. 128, 520-530.

GAMON, J.A. & PEARCY, R.W., 1989. Leaf movement, stress avoidance and photosynthesis in *Vitis californica. Oecologia* 79, 475-481.

GARCIA, A.L., TORRECILLAS, A., LEON, A. & RUIZ SANCHEZ, M.C., 1987. Biochemical indicators of water stress in maize seedlings. *Biol*. *Plant*. 29, 45-51.

GHASSEMI-GOLEZANI, K., SHEIKZADEH-MOSADEGGH, P. & VALIZADEH, M., 2008. Effects of hydropriming duration and limited duration on field performance of chick-pea. *R. J. Seed Sci*. 1, 34-40.

GIARDI, M.T., COLIA, A., GEIKEO, B., KUCERA, T., MASOJIDEK, J. & MATTO, A.K., 1996. Long-term drought stress induces structural and functional reorganization of photosystem II. *Planta* 199, 118-125.

GIRI, G.S. & SCHILLINGER, W.F., 2003. Seed priming winter wheat for germination, emergence and yield. *Crop Sci*. 43, 2135-2141.

GIROUSSE, C., BOURNITREVILLE, R. & BONNEMAIN, J.L., 1996. Water deficit-induced changes in concentration in proline and some other amino acids in the phloem sap of alfalfa. *Plant Physiol*. 111, 109-113.

GLOVER, J., 1959. The apparent behaviour of maize and sorghum stomata during and after drought. *J. Agric*. *Sci*. 53, 412-6.

GOEDHEER, J.C., 1972. Fluorescence in relation to photosynthesis. *Ann*. *Rev*. *Plant Physiol*. 23, 87-112.

GOVINDJEE, W., DOWTON, J.S., FORK, D.C. & ARMOND, P.A., 1981. Chlorophyll *a* fluorescence transient as an indicator of the water potential of leaves. *Plant Sci*. *Lett*. 20, 191-194.

GOYAL, M.R., 1982. Soil crusts vs. seedling emergence: A review: Agricultural mechanization in Asia, Africa and Latin America 13, 62-75.

GRANT, R.F., DAUGHTRY, C.S.T., KINIRY, J.R. & ARKIN, G.F., 1989. Water deficit timing effects on yield components in maize. *Agron. J*. 81, 61-65.

GREEN, T.S., ENDER, M. & MOCK, J.J., 1985. Effect of sowing dates on maize yields. *Agric. Sci*. 20, 843-850.

GUPTA, N. K., GUPTA, S. & KUMAR, A., 2001. Effect of water stress on physiological attributes and their relationship with growth and yield of wheat cultivars at different stages. *J*. *Agron*. *Crop Sci*. 186, 55-62.

GUY, R., 1982. Effects du potential osmotique sur la germination des semences de traize especes agricoles et potigens. *Schweizerische Landwirtschaftliche Forschung* 21, 21-48.

HALDER, K.P. & BURRAGE, S.W., 2004. Effect of drought stress on photosynthesis and leaf gas exchange of rice grown in Nutrient Film Technique. *Pak. J. Biol. Sci*. 7, 563-565.

HAMPTON, J.G., 1995. Methods of viability and vigour testing: A critical appraisal. In: Basra, A.S. (Ed.), Seed Quality: Basic mechanisms and implications, Food Products Press.

HAN, B. & KERMODE, A.R., 1996. Dehydrin-like proteins in castor bean seeds and seedlings are differently produced in responses to ABA and water deficit-related stresses. *J*. *Exp*. *Bot*. 47, 933-939.

HANSON, A.D., NELSON, C.E. & EVERSEN, E.H., 1977. Evolution of free proline accumulation as an index for drought resistance using two contrasting barley cultivars. *Crop Sci*. 17, 720-726.

HARRIS, D., 1992. Seedbeds and crop establishment. In: Proceedings of the Second Annual Scientific Conference of the SADCC-Land & Water Management Research Programme, October 7-9, 1991, Mbabane, Swaziland. pp 165-172

HARRIS, D., 1996. The effects of manure, genotype, seed priming, depth and date of sowing on the emergence and early growth of *Sorghum bicolor* (L.) Moench in semi-arid Botswana. *Soil Till. Res*. 40, 73–88.

HARRIS, D., FRY, G.J., MILLER, S.T. & PAIN, A., 1992. Crop production, rainfall, runoff and availability of soil moisture in semi-arid Botswana. Main final report, Land and Water Management Project, SACCAR, Gaborone, Botswana.

HARRIS, D., JOSHI, A., KHAN, P. A., GOTHKAR, P. & SODHI, P. S., 1999. On-farm seed priming in semi-arid agriculture development and evaluation in maize, rice and chickpea in India using participatory methods. *Exp. Agric*. 35, 15-29.

HARRIS, D., RAGHUWANSHI, B. S., GANGWAR, J. S., SINGH, S. C., JOSHI, K. D., RASHID, A. & HOLLINGTON, P. A., 2001. Participatory evaluation by farmers of

‘on-farm’ seed priming in wheat in India. *Nepal and Pakistan, Exp. Agric.* 37, 403–415.

HARRIS, R.E., MOLL, R.H. & STUBER, C.W., 1984. Control and inheritance of prolificacy in maize. *Crop Sci*. 16, 543-850.

HASSAN, R., 2006. Climate Change and African Agriculture. *Policy No. 28.* Based on Durand (2006), “Assessing the impact of climate change on crop water use in South Africa”, *CEEPA Discussion Paper No.28,* CEEPA, University of Pretoria.

HAVAUX, M. & LANNOYE, R., 1983. Chlorophyll fluorescence induction: a sensitive indicator of water stress in maize plants. *Irrig*. *Sci*. 4, 147-151.

HEINIGRE, R.W., 2000. Irrigation and drought management. Crop Science Department. Available from: http://www.ces.ncsu.edu/plymouth/cropsci/cornguide/Chapter4.html (Accessed 16 June 2009)

HERNANDEZ, T., 1980. Influence of Soil Moisture Content at Different Growth Stages on Yield of Maize in the State of Morelos. *Field Crop Absts*. 36, 2240.

HEUER, B., 1994. Osmoregulatory role of proline in water- and salt-stressed plants. In: Pessarakli, M. and Marcel Dekker (Eds.), Handbook of plant and crop stress, Inc. New York. pp 363.

HEYDECKER, W. & COOLBEAR, P., 1977. Seed treatments for improved seed performance - survey and attempted prognosis. *Seed Sci*. *Technol*. 5, 353- 425.

HEYDECKER, W., 1972. Vigour. In: E.H. Roberts (Ed.), Viability of seeds, London: Chapman and Hall. pp 209-252.

HEYDECKER, W.J., HIGGINS, J. & GULLIVER, K., 1973. Accelerated germination by osmotic seed treatment. *Nature* 246, 42–46.

HORTON, P., RUBAN, A.V. & WALTERS, R.G., 1996. Regulation of light harvesting in green plants. *Ann*. *Rev*. *Plant Physiol*. *Mol*. *Biol*. 47, 655-684.

HUCK, M.G., PETERSON, C.M., HOOGENBOOM, G. & BUSCH, C.D., 1986. Distribution of dry matter between shoots and roots of irrigated and non-irrigated determinate soybeans. *Agron*. *J*. 78, 807-813.

HURD, E.A., 1974. Phenotype and drought tolerance in wheat. *Agric. Meteorology* 14, 39-55.

HUTCHEON, W.L. & RANIE, D.A., 1960. The relationship of soil moisture available to the growth characteristics and quality of wheat. *Trans. 7th Int. Cong. Soil Sci.* 3, 488-495.

IBARRA-CABARELLO, J., VERDUZCO, C.V., GALAN, J.M. & JIMENEZ, E.S., 1988. Proline accumulation as a symptom of drought stress in maize: A tissue differentiation requirement. *J*. *Exp*. *Bot*. 39, 889-897.

ILAHI, I. & DORFFLING, K., 1982. Changes in abscisic acid and proline levels in maize varieties of different drought resistance. *Physiologia Plantarum* 55, 129-135.

ISTA, 1985. International Rules for Seed Testing. *Seed Sci. Technol.* 13, 299-355.

ISTA, 1995a. Handbook of vigour test methods. 3rd Ed. ISTA, Zurich.

ISTA, 2003. International Seed Testing Association, ISTA Handbook on Seedling Evaluation, 3rd Ed.

ITABARI, J.K., GREGORY, P.J. & JONES, R.K., 1993. Effects of temperature, soil water status and depth of planting on germination and emergence of maize (*Zea mays*) adapted to semi-arid eastern Kenya. *Exp. Agric*. 29, 351–364.

JONES, H.G., 1992. Plants and microclimate: A quantitative approach to environmental plant physiology. 2nd edition, Cambridge University Press.

JONES, M.J., 1987. Plant population, rainfall and sorghum production in Botswana. I. Results of experiment station trials. *Exp*. *Agric*. 23, 335-347.

JONES, M.M., TURNER, N.C. & OSMOND, C.B., 1981. Mechanisms of drought resistance. In: Paleg, L.G. and Aspinall, D. (Eds.), Physiology and biochemistry of drought resistance in plants, Academic Press. Australia. pp 15.

JUN-CHEN & DAI-JUNYING., 1996. Effect of drought on photosynthesis and grain yield of corn hybrids with different drought tolerance. *Acta-Agronomica sinica* 22, 637.

KAO, A.L., CHANG, T.Y., CHANG, S.H., SU, J.C. & YANG, C.C., 2005. Characterisation of a novel *Arabidopsis* protein family AtMAPR homologous to 25-Dx/IZAg/Hpr6.6 proteins. *Bot. Bull. Acad. Sin*. 46, 107-118.

KATERJI, N., VAN HOORN, J.W., HAMDY, A., KARAM, F. & MASTRORILLI, M., 1994. Effect of salinity on emergence and on water stress and early seedling growth of sunflower and maize. *Agricultural Water Management* 26, 81-91.

KAUTSKY, H., APPEL, W. & AMANN, H., 1960. Chlorophyll fluorescenzund kohlesaureassimilation. *Biochemische Zeitschrift* 322, 277-292.

KEMBLE, A.R. & MACPHERSON, H.T., 1954. Liberation of amino acids in perennial ryegrass during wilting. *Biochem. J*. 58, 46.

KHAJEH-HOSSEINI, M., POWELL, A.A. & BINGHAM, I.J., 2003. The interaction between salinity stress and seed vigour during germination of soybean seeds. *Seed Sci. Technol.* 31, 715-725.

KHAN, M.B., HUSSAIN, N. & IQBAL, M., 2001. Effect of water stress on growth and yield components of maize variety YHS202. *J. Res. (Science)* 12, 15-18.

KHANNACHOPRA, R. & KUMARI, S., 1995. Influence of various amounts of irrigation water and nitrogen fertiliser on growth, yield and water-use of grain sorghum. *J. Agron. Crop Sci.* 174, 151-161.

KIBITE, S. & HARKER, K. N., 1991. Effects of seed hydration on agronomic performances of wheat, barley and oats in central Alberta. *Can. J. Plant Sci*. 71, 515-518.

KRAMER, P.J. & BOYER, J.S., 1995. Water relations of plants and soils. Academic Press Inc. pp 136-140; 383-389.

KRAMER, P.J., 1983. Water relations of plants. New York, pp 489.

KRAUSE, G.H. & WEIS, E., 1991. Chlorophyll fluorescence and photosynthesis: the basis. *Ann. Rev. Plant Physiol*. 136, 472-479.

KUMAR, A., SINGH, D.P. & SINGH, P., 1994. Influence of water stress on photosynthesis, transpiration, water use efficiency and yield of *Brassica juncea* L. *Field Crops Res.* 37, 95-101.

LAEMMILI, U.K., 1970. Cleavage of structural proteins during assembly of the head of bacteriophage T4. *Nature* 227, 680-685.

LAL, A. & EDWARDS, G.E., 1996. Analysis of inhibition of photosynthesis in the C4 species *Amaranthus cruentus* and *Zea mays*: electron transport, CO_2 fixation and carboxylation capacity. *Aust. J. Plant Physiol*. 23, 403-412.

LAUER, J., 2003. What happens within the corn plant when drought occurs? University of Wisconsin Extension. Available from: http://www.uwex.edu/ces/ag/issues/drought2003/cornseffect.html (Accessed 16 June 2009).

LAUER, J.G., CARTER, P.R., WOOD, T.M., DIESEL, G., WIERSMA, D.W., RAND, R.E. & MLYNAREK, M.J., 1999. Corn hybrid response to planting date in the Northern Corn Belt. *Agron. J.* 91, 834-839.

LAWLOR, D. W., 2002. Limitation to photosynthesis in water-stressed leaves: Stomata *vs*. metabolism and the role of ATP. *Ann*. *Bot*. 89, 871-885.

LEHTO, T. & GRACE, J., 1994. Carbon balance of tropical tree seedlings: A comparison of two species. *New Phytologist* 127, 455-463.

LEMON, E.R., 1966. Energy conversion and water use efficiency. In: W.H. Pierre *et al.* (Ed.), Plant environment and efficient water use, Madison, Wis: American Society of Agronomy Publication. pp 22-48

LI, X., FENG, Y. & BOERSMA, L., 1994. Partition of photosynthates between shoot and root in spring wheat (*Triticum aestivum* L.) as a function of soil water potential and root temperature. *Plant and Soil* 164, 43-50.

LU, Q., LU, C., ZHANG, J. & KUANG, T., 2002. Photosynthesis and chlorophyll fluorescence during flag leaf senescence of field grown wheat plants. *J. Plant Physiol.* 159, 1173-1178.

LUDLOW, M.M. & MUCHOW, R.C., 1990. A critical evaluation of traits for improving yield in water limited environments. *Adv. Agron.* 43, 107-153.

LUNA, C.M., PASTORI, G.M., DRISCOLL, S., GROTON, K., BERNARD, S. & FOYER, C.H., 2004. Drought controls on H_2O_2 accumulation, catalase (CAT) activity and *CAT* gene expression in wheat. *J. Exp. Bot*. 56, 417-423.

MAGUIRE, J.D., 1962. Speed of germination - aid in selection and evaluation for seedling emergence and vigour. *Crop Sci.* 2, 176-177.

MAITI, R., 1996. Sorghum science. Science Publishers, Lebanon, New Hampshire. pp 352.

MARCELIS, L. F. M., HEUVELINK, E. & GOUDRIAAN, J., 1998. Modelling biomass production and yield of horticultural crops: A review. *Scientia Hort.* 74, 83-111.

MASOJIDEK, J., TRIVEDI, S., HALSBOW, L., ALEXIOU, A. & HALL, D.O., 1991. The synergistic effect of drought and light stresses in sorghum and pearl millet. *Plant Physiol.* 96, 198-207.

MATARIRA, C.H., MAKADHO, J.C. & MUKAHANANA-SANGARWE, M., 2004. Vulnerability and adaptation of maize production to climate change in Zimbabwe. Ministry of Environment and Tourism, Zimbabwe

MATTHEWS, S. & POWELL, A.A., 1986. Environmental and physiological constraints on field performance of seeds. *Hort. Sci.* 21, 893-899.

MAXWELL, K. & JOHNSON, G.N., 2000. Chlorophyll fluorescence- a practical guide. *J. Exp. Bot*. 51, 659-668.

McCANN, J., 2005. Maize and Grace: Africa's encounter with a new crop, 1500-2000. Harvard University Press, New York.

McDONALD, M. B., 2000. Seed priming. In: Black, M., J. D. Bewley. (Eds.), Seed technology and its biological basis, Sheffield Academic Press, Sheffield, UK, pp 287–325.

MEDRANO, H., ESCALONA, J. M., BOTA, J., GULIAS, J. & FLEXAS, J., 2002. Regulation of photosynthesis of C3 plants in response to progressive drought. Stomatal conductance as a reference parameter. *Ann. Bot*. 89, 895-905.

MILTHORPE, F.L., (Ed.) 1956. The growth of leaves, Proceed Univ. Nottingham, Third Easter School in Agric. Sci. London, Butterworth Publishers. pp 223

MIRACLE, M.J., 1966. Maize in tropical Africa. Madison, WI: University of Wisconsin Press.

MITTOVA, V., TAL, M., VOLOKITA, M. & GUY, M., 2002. Salt stress induces upregulation of an efficient chloroplasts antioxidant system in the salt-tolerant wild tomato species *Lycopersicon pennellii* but not the cultivated species. *Plant Physiol.* 115, 393-400.

MODI, A.T., 2004. Short-term preservation of maize landrace seed and taro propagules using indigenous storage methods. *S.A. J. Bot*. 70, 16-22.

MOHAMMADKHANI, N. & HEIDARI, R., 2008. Effects of drought stress on protective enzyme activities and lipid peroxidation in two maize cultivars. *Pak. J. Biol. Sci*. 10, 3835-3840.

MONTEITH, J.L & ELSTON, J., 1983. Performance and productivity of foliage in the field. In: J.E. Dale and F.L Milthorpe. (Eds.), The growth and functioning of leaves, Cambridge University Press. pp 409-518.

MU-QING, Z., CHEN, R., LUO, J., LU, J. & XU, J., 2000. Analysis of inheritance and combining ability of photochemical activities measured by chlorophyll fluorescence in the segregating generation of sugarcane. *Field Crops Res*. 65, 31-39.

MUSIK, J.T. & DUSEK, D.A., 1980. Irrigated corn yield response to water. *Trans. ASAE* 23, 92-98, 103.

MWALE, S.S., HAMUSIMBI, S. & MWANSA, K., 2003. Germination, emergence and growth of sunflower (*Helianthus annus* L.) in response to osmotic seed priming. *Seed Sci. Technol*. 31, 199-206.

NAGAR, R.P., DADLAN, M.I. & SHARAMA, S.P., 1998. Effect of hydropriming on field emergence and crop growth of maize genotypes. *Seed Res*. 26, 1-5.

NAIDU, B.P., PULEG, L.G., ASPINALL, D., JENNING, A.C. & JONES, G.P., 1990. Rate of imposition of water stress alters the accumulation of nitrogen containing solutes by wheat seedlings. *Aust. J. Plant Physiol*. 17, 377.

NAM, N.H., SUBBARAO, G.V., CHAUHAN, Y.S. & JOHANSEN, C., 1998. Importance of canopy attributes in determining dry matter accumulation of pigeon pea under contrasting moisture regimes. *Crop Sci*. 38, 955-961.

NIELSON, R.L., 2005 (Rev. Aug 2008). Kernel Set Scuttlebut. www.kingcorn.oorg/news/timeless/KernelSet.html (Accessed 20/03/2009).

NOCTOR, G. & FOYER, C.H., 1998. Ascorbat and glutathione: Keeping active oxygen under control. *Ann. Rev. Plant Physiology. Plant Mol. Biol.* 49, 249-279.

NOCTOR, G., VELJOVIC-JOVANOVIC, S.D., DRISCOLL, S., NOVITSKAYA, L. & FOYER, C.H., 2002. Drought and oxidative load in wheat leaves. A predominant role for photorespiration? *Ann. Bot*. 89, 841–850.

NORWOOD, C.A., 2001. Dryland corn production in Western Kansas: Effect of hybrid maturity, planting date and plant population. *Agron. J*. 93, 540-547.

OBENG-ANTWI, K., SALLAH, P.Y.K., & FRIMPONG-MANSO, P.P., 2002. Research efforts at managing production in lowland tropics. *Ghana J. Agric. Sci.* pp 35.

OFORI, E. & KYEI-BAFFOUR, N., 2008. Chapter 13C: Agrometeorology and Maize Production. www.agrometeorology.org/fileadmin/insam/repository/chapter13c. (Accessed June, 2008).

OKONWO, J.C. & VANDERLIP, R.L., 1985. Effect of cultural treatment on quality and subsequent performance of pearl millet seed. *Field Crops Res*. 11, 161-170.

OTEGUI, M. & MELON, S., 1997. Kernel set and flower synchrony within the ear of maize: I. Sowing date effects. *Crop Sci*. 37, 441-447.

OTEGUIE, M.E., NICOLINI, M.G., RUIZ, R.A. & DODDS, P.A., 1995. Sowing date effects on grain yield components for different maize genotypes. *Agron. J*. 87, 29-33.

PAN, X.Y., WANG, Y.F., WANG, G.X., CAO, Q.D. & WANG, J., 2002. Relationship between growth redundancy and size inequality in spring wheat populations mulched with clear plastic film. *Acta Phytoecol. Sinica* 26, 177-184.

PASTORI, G.M. & FOYER, C.H., 2002. Common components, networks and pathways of cross-tolerance to stress. The central role of 'redox' and abscisic-acid-mediated controls*. Plant Physiol*.129, 460–468.

PECAD, 2003. Production estimates and crop assessment division. South African Corn Production.

http://www.fas.usda.gov/pecad2/highlights/2001/02/SAfrica/02.htm (Accessed 20 June 2009).

PEI, Z.M., MURATA, Y., BENNING, G., THOMINE, S., KLÜSENER, B., ALLEN, G.J., GRILL, E. & SCHROEDER, J.I., 2000. Calcium channels activated by hydrogen peroxide mediate abscisic acid signalling in guard cells. *Nature* 406, 731–734.

PERRY, D.A., 1972. Seed vigour and field establishment. *Hort. Abstr.* 42, 334-342.

PERRY, D.A., 1976. Seed vigour and seedling establishment. *Adv. Res. Tech. Seeds* 2, 62-85.

PERRY, D.A., 1978. Report on the vigour test committee 1974-1977. *Seed Sci. Technol*. 6, 159-181.

PERRY, D.A., 1980. Seed vigour and seedling establishment. *Adv. Res. Tech. Seeds* 5, 25-40.

PERRY, D.A., 1982. The influence of seed vigour on vegetable seedling establishment. *Sci. Hort.* 33, 67-75.

PIC, E., TEYSSENDIER DE LA SERVE, B., TARDIEU, F. & TURC, O., 2002. Leaf senescence induced by mild water deficit follows the same sequence of macroscopic, biochemical, and molecular events as monocarpic senescence in pea*. Plant Physiol.* 128, 236-246.

PIETA- FILHO, C. & ELLIS, R.H., 1991. The development of seed quality in spring barley in four environments. a. Germination and longevity. *Seed Sci. Res.* 1, 163-177.

POLLOCK, B.M., 1969. Imbibition temperature sensitivity of lima beans controlled by initial seed moisture. *Plant Physiol*. 44, 907-911.

PORRO, I. & CASSEL, D.K., 1986. Response of maize to tillage and delayed irrigation. *Field Crop Abstr*. 40, 637.

POWELL, A.A. & MATHEWS, S., 1978. The damaging effect of water on dry pea embryos during imbibition. *J. Exp. Bot*. 29, 1215–1229.

POWELL, A.A., 1988. Seed vigour and field establishment. *Adv. Res. Tech. Seeds.* 11, 29-61.

POWELL, A.A., MATTHEWS, S. & OLIVEIRA, M. DE A., 1984. Seed quality in grain legumes. *Adv. App. Bio.* 10, 217-285.

PRUSINSKI, J. & KHAN, A.A., 1990. Relationship of ethylene production to stress alleviation in seeds of lettuce cultivars. *J. American. Soc. Hort. Sci.* 115, 294-298.

PUGNAIRE, I. F., SERRANO, L. & PARDOS, J., 1999. Constraints by water stress on plant growth. In: Pessarakli, M. (Ed.), Handbook of plant and crop stress, 2nd edition, revised and expanded. Marcel Dekker, New York, pp. 271-283.

RADHOUANE, L., 2007. Response of Tunisian autochthonous pearl millet (*Pennisetum glaum* L. R.Br.) to drought stress induced by polyethylene glycol (PEG) 6000. *Afri. J. Biotec*. 6, 1102-1105.

RANDHIR, R. & SHETTY, K., 2003. Light-mediated fava bean (*Vicia faba*) response to phytochemical and protein elicitors and consequences on nutraceutrical enhancement and seed vigour. *Process Biochem*. 38, 945-952.

RATCLIFFE, D., 1974. Adaptation to habitat in a group of annual plants. *J. Eco.* 49, 187-203.

RAUF, M., MUNIR, M., HASSAN, M., AHMAD, M. & AFZAL, M., 2007. Performance of wheat genotypes under osmotic stress at germination and early seedling growth stage. *Afri. J. Biotech*. 6, 971-975.

RICCARDI, F.P., GAZEAU, D. DE VIENNE & ZIVY, M., 1998. Protein changes in response to progressive water deficit in maize. *Plant Physiol*. 117, 1253-1263.

ROWLAND, J.R.J., 1993. Dryland farming in Africa. Macmillan Press Limited, London.

RUSSELL, M.B., 1959. Water and its relation to soils and crop. *Adv. Agron*. 11, 1-122.

SADRAS, V.O., VILLALOBOS, F.J. & FERERES, E., 1993. Leaf expansion in field-grown sunflower in response to soil and leaf water status. *Agron. J*. 85, 564-570.

SAMARAS, Y., BRESSAN, R.A., CSONKA, L.N., GARCIA-RIOS, M., D'URZO, M. & RHODES, D., 1995. Proline accumulation during water deficit. In: Smirnoff N.

(Ed.), Environment and plant metabolism. Flexibility and acclimation. Oxford: Bios Scientific Publishers.

SANCHEZ, R.A., HALL, A.J. & COHEN DE HUNAU, R., 1983. Effects of water stress on the chlorophyll content, nitrogen level and photosynthesis of leaves of two maize genotypes. *Photosynth. Res*. 4, 35-47.

SANGAKKARA, U.R., 1998. Growth and yields of cowpea (*Vigna unguiculata* (L.) Walp) as influenced by seed characters, soil moisture and season of planting. *J. Agron. Crop Sci.* 180, 137-142.

SANGAKKARA, U.R., HARTWIG, U.A. & NÖSBERGE, J., 1996a. Response of root branching and shoot water potentials of French bean (*Phaseolus vulgaris* L.) to soil moisture and fertilizer potassium. *J. Agron. Crop Sci.* 177, 165-173.

SANGAKKARA, U.R., HARTWIG, U.A. & NÖSBERGER, J., 1996b. Root and shoot development of *Phaseolus vulgaris* L. (French beans) as affected by soil moisture and fertilizer potassium. *J. Agron. Crop Sci*. 177, 145-151.

SCANDALIOS, J.G., GUAN, L. & POLIDOROS, A.N., 1997. Catalases in plants: gene structure, properties, regulation and expression. In: Scandalios, J.G. (Ed.), Oxidative stress and the molecular biology of antioxidants defences, New York, Cold Spring Harbor Laboratory Press. pp 343–406.

SCBREIBER, U. & BILGER, W., 1993. Progress in chlorophyll fluorescence research: Major developments during the past years in retrospect. In: Behnke, H.D., U. Luttge, K. Esser, J.W. Kadereit and M. Runge. (Eds.), Progress in botany. Vol. 54. Springer, Berlin Heidelberg, New York, pp151-173.

SCHREIBER, U., BILGER, W. & NEUBAUER, C., 1994. Chlorophyll fluorescence as a non-intrusive indicator for rapid assessment of in vivo photosynthesis. In

Schulze, E.D., Caldwell, M.M. (Eds.), Ecophysiology of photosynthesis. (Ecological Studies, vol 100) Springer, Berlin Heidelberg, New York, pp 49-70.

SCHUSSLER, J.R. & WESTGATE, M.E., 1991. Maize kernel set at low water potential: I. Sensitivity to reduced assimilates during early kernel growth. *Crop Sci*. 31, 1189-1195.

SHARP, R.E., SILK, W.K. & HSIAO, T.C., 1988. Growth of the maize primary root at low water potentials. I. Spatial distribution of expansive growth. *Plant Physiol*. 87, 50-57.

SHAW, R.H., 1974. A weighted moisture stress index for corn in Iowa. *Iowa State J. Res.* 49, 101-114.

SHAW, R.H., 1977. Water use and requirements of maize - a review. Agrometeorology of the maize (corn) crop. 486. World Met. Organization Publication. pp 119-134.

SHEPERD, L.N., HICKS, D.R. & SCHMIDTH, W.H., 1991. Maximising the advantages of early corn planting. National Corn Handbook, Crop Management. Purdue University Cooperative Extension Service. West Lafayette, Indiana. NCH-35.

SHTREVA, L. ATANASSOVA, B., KARCHEVA, T. & PETKOV, V., 2008. The effect of water stress on growth rate, water content and proline accumulation in Tomato calli and seedlings. *Proc. XVth EUCARPIA Tomato. Acta Hort. 789, ISHS*.

SIKANDAR, A., ALI, M., AMIN, M., BIBI, S., & ARIF, M., 2007. Effect of plant population on maize hybrids. *J. Agric. Biol. Sci*. 2:

SINGH, P., 1991. Influence of water deficits on phenology, growth and dry-matter allocation in chickpea (*Cicer arietinum*). *Field Crops Res.* 28, 1-15.

SMIRNOFF, N. & CUMBES, Q.J., 1989. Hydroxyl radical scavenging activity of compatible solutes. *Phytochemistry* 28, 1057-1060.

SMIRNOFF, N. & STEWART, G.R., 1985. Stress metabolites and their role in coastal plants. *Vegetation* 62, 273-278.

SOUTH AFRICAN WEATHER SERVICES, 2008. Drought mitigation desk. Available from: http://www.weathersa.co.za/DroughtMonitor/MetDrought.jsp. (Accessed June, 2008).

SRIVALLI, B., SHARMA, G. & KHANNA-CHOPRA, R., 2003. Antioxidant defense system in an upland rice cultivar subjected to increasing intensity of water stress followed by recovery. *Plant Physiol.* 119, 503-512.

STOSKOPF, C.N., 1981. Understanding crop production. Reston Publishing Company, Inc., Reston, Virginia. pp 91-99.

SUBEDI, K.D. & MA, B.L., 2005. Seed priming does not improve corn Yield in a humid temperate environment. *Agron. J*. 97, 211-218.

SUN, C.J., LIU, Z.G. & JING, Y.D., 2003. Effect of water stress on activity and isozyme of the major defense enzyme in maize leaves. *J. Maize Sci.* 11, 63-66.

TAIZ, L. & ZEIGER, E., 2006. Plant Physiology, 4th edition. Sinauer Associates, Inc., Publishers. Sunderland Massachusetts. pp 671-76.

TAYLOR, A.G., PRUSINSKI, J., HILL, H.J. & DICKSON, M.D., 1992. Influence of seed hydration on seedling performance. *Hort. Technol.* 2, 336–344.

TAYLOR, H.M. & BLACKETT, P.S., 1982. Soybean and maize yield as affected by row spacing, planting dates and seasonal water supply. *Agron. J*. 80, 930-935.

TEKRONY, D.M. & EGLI, D.B., 1991. Relationship of seed vigour to crop yield: A review. *Crop Sci.* 31, 816-822.

THELEN, K., 2007. Assessing drought stress effects on corn yield. www.ipm.msu.edu/cat07field/fc06-28-07html (Accessed 19/03/2009).

TI-DA, G.E., FANG-GONG, S.O.I., PING, B.A.I.L.I., YIN-YAN, L.U. & GUANG-SHENG, Z., 2006. Effect of water stress on the protective enzymes and lipid peroxidation in roots and leaves of summer maize. *Agric. Sci. China* 5, 291-298.

TOLLENAAR, M. & AGUILERA, A., 1992. Radiation use efficiency of an old and a new maize hybrid. *Agron. J.* 84, 536-541.

TURC, O. & LECOEUR, J., 1997. Leaf primordium initiation and expanded leaf production are co-ordinated through similar response to air temperature in pea (*Pisum sativum* L.). *Ann. Bot*. 80, 265-273.

TURNER, L.B., 1991. The effect of water stress on vegetative growth of white clover (*Trifolium repens* L.): Comparison of long-term water deficit and short-term developing water stress. *J. Exp. Bot.* 42, 311-316.

VAIDYANATHAN, H., SIVAKUMAR, P., CHAKRABARTY, R. & THOMAS, G., 2003. Scavenging of reactive oxygen species in NaCl-stressed rice (*Oryza sativa* L.) differential response in salt-tolerant and sensitive varieties. *Pl. Sci.* 165, 1411-1418.

VALENTINUZ, O.R., 2002. Leaf senescence and the profile of expanded leaf area in maize (*Zea Mays* L). PhD Dissertation, University of Guelph, Guelph, Canada. pp 114.

VAZAN, S., 2002. Effects of chlorophyll parameters and photosynthesis efficiency in different beet. Assay PhD Islamic Azad University Science and Research Tehran-Branch. pp 285.

VERSLUES, P.E. & SHARP, R.E., 1999. Proline accumulation in maize (*Zea mays* L.) primary roots at low water potentials. II. Metabolic source of increased proline deposition in the elongation zone. *Plant Physiol*.119, 1349–1360.

WAHID, A. & SHABBIR, A., 2005. Induction of heat stress tolerance in barley seedlings by pre-sowing seed treatment with glycinebetaine. *Plant Growth Regul.* 46, 133-141.

WAHID, A., NOREEN, A., BASRA, S.M.A., GELANI, S. & FAROOQ, M., 2008. Priming induced metabolic changes in sunflower (*Helianthus annuus*) achenes improve germination and seedling growth. *Bot. Studies* 49, 343-350.

WAHID, A., PARVEEN, M., GELANI, S. & BASRA, S.M.A., 2007. Pre-treatment of seeds with H_2O_2 improves salt tolerance of wheat seedling by alleviation of oxidative damage and expression of stress proteins. *J. Plant Physiol*. 164, 283-294.

WANG, J., LI, D.Q. & GU, L.S., 2002. The response to water stress of the antioxidant system in maize seedling roots with different drought resistance. *Acta Bot. Boreali-Occidentalia Sinica* 22, 285-290.

WELTZIEN, H.C. & SRIVASTAVA, J.P., 1981. Stress factors and barley productivity and their applications in breeding strategies. ICARDA, Alepo (Syria). In barley genetics IV, Fourth Int. Barley Generics Symposium, Edinburgh, Scotland. pp 351-369.

WESLEY B. B., EDMEADES, G.O. & BARKER, T.C., 2002. Molecular and physiological approaches to maize improvement for drought tolerance. *J. Exp. Bot.* 53, 13-25.

WIEN, H.C., 1997. Correlative growth in vegetables. In: Wien, H. C (Ed.), The physiology of vegetable crops. CAB international, pp 181-206.

WILSON, B.J., 1988. A review of evidence on the control of shoot to root ratio, in relation to models. *Ann. Bot*. 61, 433-449.

WINDAUER, L., ALTUNA, A. & BENECH-ARNOLD, R., 2007. Hydrotime analysis of *Lesquerella fendleri* seed germination responses to priming treatments. Indus. *Crop Prod*. 25, 70-74

YANCEY, P.H., CLARK, M.E., HAND, S.C., BOWLUS, R.D. & SOMERO, G.N., 1982. Living with water stress: evolution of osmolyte systems. *Science* 217, 1214–1222.

YOUNG, K.J. & LONG, S.P., 2000. Crop ecosystem responses to climate change: Maize and Sorghum. In: Reddy, K.R. and Hodges, H.F. (Eds.), Climate change and global crop productivity, CAB International Publishing. pp 107-131.

ZEVEN, A.C., 1998. Landraces: A review of definitions and classifications. *Euphytica* 104, 127-139.

ZULINI, L., RUBINIG, M., ZORER, R. & BERTAMINI, M., 2007. Effects of drought stress on chlorophyll fluorescence and photosynthetic pigments in Grapevine Leaves (*Vitis vinifera* cv. 'White Riesling'). Proc. Intl. WS on Grapevine. (Eds.) V. Nuzzo *et al*. *Acta Hort*. 754, 289-294.

APPENDICES

Appendix 1: List of ANOVAs for Early Establishment Trial

Variate: % Germ

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replicate stratum	3	125.00	41.67	1.57	
Replicate.*Units* stratum					
Genotype	3	4107.86	1369.29	51.56	<.001
Day	6	132185.71	22030.95	829.62	<.001
Variety*Day	18	14477.14	804.29	30.29	<.001
Residual	81	2151.00	26.56		
Total	111	153046.71			

Variate: Root length (mm)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Genotype	3	9328.3	3109.4	3.27	0.032
Residual	36	34232.5	950.9		
Total	39	43560.8			

Variate: Shoot length (mm)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Genotype	3	6874.5	2291.5	6.70	0.001
Residual	36	12310.6	342.0		
Total	39	19185.1			

Variate: root:shoot

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Genotype	3	5.3092	1.7697	5.48	0.003
Residual	36	11.6349	0.3232		
Total	39	16.9440			

Variate: Dry mass (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Genotype	3	0.052167	0.017389	4.37	0.010
Residual	36	0.143210	0.003978		
Total	39	0.195378			

Variate: EC

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Cell stratum	99	19751278.	199508.	1.01	
Cell.*Units* stratum					
Genotype	3	5743874.	1914625.	9.73	<.001
Residual	297	58456850.	196824.		
Total	399	83952002.			

Variate: GVI

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replicate stratum	3	22.608	7.536	3.37	
Replicate.*Units* stratum					
Genotype	3	1784.103	594.701	265.62	<.001
Day	6	12453.277	2075.546	927.04	<.001
Variety*Day	18	306.235	17.013	7.60	<.001
Residual	81	181.350	2.239		
Total	111	14747.573			

Variate: MGT(days)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replication stratum	3	0.007500	0.002500	0.47	
Replication.*Units* stratum					
Genotype	3	0.802500	0.267500	50.68	<.001
Residual	9	0.047500	0.005278		
Total	15	0.857500			

Variate: % Emerged

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replication stratum	2	8.33	4.17	0.12	
Replication.*Units* stratum					
F.Capacity	1	30459.38	30459.38	867.32	<.001
Genotype	3	386.46	128.82	3.67	0.039
F. Capacity*Genotype	3	353.12	117.71	3.35	0.050
Residual	14	491.67	35.12		
Total	23	31698.96			

Variate: MET(days)

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		2.2243	1.1122	7.04	
Rep.*Units* stratum						
Genotype	3		3.4105	1.1368	7.20	0.015
F.Capacity	1		63.1370	63.1370	399.81	<.001
Genotype*F.Capacity	3		1.4606	0.4869	3.08	0.099
Residual	7	(7)	1.1054	0.1579		
Total	16	(7)	46.4065			

Variate: Root length (mm)

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		1349.46	674.73	9.34	
Rep.*Units* stratum						
Genotype	3		575.91	191.97	2.66	0.106
F.Capacity	1		369.33	369.33	5.11	0.047
Genotype*F.Capacity	3		855.23	285.08	3.95	0.043
Residual	10	(4)	722.58	72.26		
Total	19	(4)	2929.80			

Variate: Shoot length (mm)

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		1178.9	589.5	0.62	
Rep.*Units* stratum						
Genotype	3		3163.8	1054.6	1.11	0.390
F.Capacity	1		35468.3	35468.3	37.36	<.001
Genotype*F.Capacity	3		11002.1	3667.4	3.86	0.045
Residual	10	(4)	9494.1	949.4		
Total	19	(4)	56781.0			

Variate: root:shoot

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		0.076380	0.038190	4.86	
Rep.*Units* stratum						
Genotype	3		0.086706	0.028902	3.68	0.051
F.Capacity	1		0.137993	0.137993	17.55	0.002
Genotype*F.Capacity	3		0.103994	0.034665	4.41	0.032
Residual	10	(4)	0.078608	0.007861		
Total	19	(4)	0.350470			

Variate: Leaf area (cm^2)

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		655.68	327.84	4.40	
Rep.*Units* stratum						
Genotype	3		56.67	18.89	0.25	0.857
F.Capacity	1		3090.88	3090.88	41.44	<.001
Genotype*F.Capacity	3		1085.90	361.97	4.85	0.025
Residual	10	(4)	745.92	74.59		
Total	19	(4)	5493.30			

Variate: Plant height (cm)

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		625.24	312.62	3.35	
Rep.*Units* stratum						
Genotype	3		956.67	318.89	3.41	0.082
F.Capacity	1		32273.14	32273.14	345.58	<.001
Genotype*F.Capacity	3		3244.43	1081.48	11.58	0.004
Residual	7	(7)	653.73	93.39		
Total	16	(7)	24208.94			

Variate: Leaf no.

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		0.6404	0.3202	1.40	
Rep.*Units* stratum						
Genotype	3		1.0222	0.3407	1.49	0.298
F.Capacity	1		23.9963	23.9963	104.98	<.001
Genotype*F.Capacity	3		2.5129	0.8376	3.66	0.071
Residual	7	(7)	1.6000	0.2286		
Total	16	(7)	18.4706			

Appendix 2: ANOVA for Proline Study

Variate: Proline Concentration (µg/gDW)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	0.00250806	0.00125403	55.00	
Rep.*Units* stratum					
Variety	3	0.26501562	0.08833854	3874.24	<.001
F.Capacity	1	3.22604267	3.22604267	1.415E+05	<.001
Variety*F.Capacity	3	0.11387366	0.03795789	1664.71	<.001
Residual	14	0.00031922	0.00002280		
Total	23	3.60775922			

Appendix 3: List of ANOVAs for Controlled Experiment Study

Variate: Daily Emergence (%)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replication stratum	2	3371.9	1686.0	5.41	
Replication.*Units* stratum					
F.Capacity	1	783.7	783.7	2.51	0.115
Variety	3	7540.4	2513.5	8.06	<.001
DAS	9	323116.4	35901.8	115.12	<.001
F. Capacity*Variety	3	3981.5	1327.2	4.26	0.006
F. Capacity*DAS	9	1674.0	186.0	0.60	0.799
Variety*DAS	27	9101.2	337.1	1.08	0.369
F. Capacity*Variety*DAS	27	4872.4	180.5	0.58	0.952
Residual	158	49275.6	311.9		
Total	239	403716.9			

Variate: Final Emergence (%)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replication stratum	2	1204.6	602.3	1.78	
Replication.*Units* stratum					
Variety	3	3156.3	1052.1	3.11	0.060
F.Capacity	1	185.9	185.9	0.55	0.471
Variety*F. Capacity	3	1670.0	556.7	1.65	0.224
Residual	14	4733.9	338.1		
Total	23	10950.8			

Variate: MET (days)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replication stratum	2	0.08120	0.04060	0.49	
Replication.*Units* stratum					
Variety	3	0.26616	0.08872	1.06	0.396
F.Capacity	1	0.00135	0.00135	0.02	0.901
Variety*F. Capacity	3	0.05503	0.01834	0.22	0.881
Residual	14	1.16868	0.08348		
Total	23	1.57243			

Variate: Plant Height (cm)

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		292.3	146.1	1.07	
Rep.*Units* stratum						
FC	1		31600.9	31600.9	231.43	<.001
Variety	3		4571.9	1524.0	11.16	<.001
Week	7		705885.5	100840.8	738.51	<.001
FC*Variety	3		139.2	46.4	0.34	0.797
FC*Week	7		23439.0	3348.4	24.52	<.001
Variety*Week	21		5317.5	253.2	1.85	0.020
FC*Variety*Week	21		1881.6	89.6	0.66	0.868
Residual	125	(1)	17068.2	136.5		
Total	190	(1)	780236.7			

Variate: Leaf No.

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		6.5820	3.2910	7.00	
Rep.*Units* stratum						
FC	1		42.3513	42.3513	90.08	<.001
Variety	3		5.5157	1.8386	3.91	0.010
Week	7		2374.1314	339.1616	721.35	<.001
FC*Variety	3		3.6678	1.2226	2.60	0.055
FC*Week	7		32.7333	4.6762	9.95	<.001
Variety*Week	21		5.3969	0.2570	0.55	0.945
FC*Variety*Week	21		16.5860	0.7898	1.68	0.042
Residual	125	(1)	58.7717	0.4702		
Total	190	(1)	2505.3717			

Variate: Fv/Fm

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		0.0016209	0.0008105	2.14	
Rep.*Units* stratum						
Variety	3		0.0035392	0.0011797	3.12	0.031
FC	1		0.0012359	0.0012359	3.26	0.075
DAP	4		0.0051029	0.0012757	3.37	0.014
Variety*FC	3		0.0001057	0.0000352	0.09	0.964
Variety*DAP	12		0.0021571	0.0001798	0.47	0.923
FC.DAP	4		0.0025598	0.0006399	1.69	0.161
Variety*FC*DAP	12		0.0056386	0.0004699	1.24	0.273
Residual	74	(4)	0.0280233	0.0003787		
Total	115	(4)	0.0492717			

Variate: Final Plant Height (cm)

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		527.6	263.8	0.68	
Rep.*Units* stratum						
FC	1		23188.2	23188.2	60.08	<.001
Variety	3		3483.3	1161.1	3.01	0.069
FC*Variety	3		551.2	183.7	0.48	0.704
Residual	13	(1)	5017.1	385.9		
Total	22	(1)	32299.8			

Variate: Final Leaf No.

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		4.9184	2.4592	2.48	
Rep.*Units* stratum						
FC	1		0.0306	0.0306	0.03	0.863
Variety	3		5.2823	1.7608	1.77	0.202
FC*Variety	3		8.4252	2.8084	2.83	0.080
Residual	13	(1)	12.9048	0.9927		
Total	22	(1)	29.7391			

Variate: Final Fv/Fm

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
Rep stratum	2		0.0011918	0.0005959	1.66	
Rep.*Units* stratum						
FC	1		0.0018525	0.0018525	5.16	0.041
Variety	3		0.0022213	0.0007404	2.06	0.155
FC*Variety	3		0.0016430	0.0005477	1.53	0.255

Residual	13	(1)	0.0046663	0.0003589
Total	22	(1)	0.0109406	

Variate: No. of Ears

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replication stratum	2	0.3333	0.1667	0.37	
Replication.*Units* stratum					
F.Capacity	1	0.0417	0.0417	0.09	0.766
Variety	3	7.1250	2.3750	5.25	0.012
F. Capacity*Variety	3	3.1250	1.0417	2.30	0.122
Residual	14	6.3333	0.4524		
Total	23	16.9583			

Variate: Ear length (cm)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replication stratum	2	52.56	26.28	1.16	
Replication.*Units* stratum					
F.Capacity	1	40.51	40.51	1.79	0.202
Variety	3	264.46	88.15	3.90	0.032
F. Capacity*Variety	3	1.38	0.46	0.02	0.996
Residual	14	316.67	22.62		
Total	23	675.58			

Variate: Ear mass (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replication stratum	2	5214.0	2607.0	3.73	
Replication.*Units* stratum					
F.Capacity	1	10796.7	10796.7	15.44	0.002
Variety	3	9550.1	3183.4	4.55	0.020
F. Capacity*Variety	3	8411.9	2804.0	4.01	0.030
Residual	14	9790.1	699.3		
Total	23	43762.8			

Variate: Kernel rows/ear

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replication stratum	2	43.896	21.948	2.85	
Replication.*Units* stratum					
F.Capacity	1	110.510	110.510	14.33	0.002
Variety	3	49.781	16.594	2.15	0.139
F. Capacity*Variety	3	105.865	35.288	4.58	0.020

Residual	14	107.938	7.710		
Total	23	417.990			

Variate: Kernel number/ear

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replication stratum	2	15343.	7672.	3.44	
Replication.*Units* stratum					
F.Capacity	1	27032.	27032.	12.12	0.004
Variety	3	16703.	5568.	2.50	0.102
F. Capacity*Variety	3	18679.	6226.	2.79	0.079
Residual	14	31216.	2230.		
Total	23	108973.			

Variate: Grain mass (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Replication stratum	2	2358.1	1179.0	1.65	
Replication.*Units* stratum					
F.Capacity	1	10203.6	10203.6	14.29	0.002
Variety	3	6431.2	2143.7	3.00	0.066
F. Capacity*Variety	3	6666.2	2222.1	3.11	0.060
Residual	14	9994.4	713.9		
Total	23	35653.4			

Appendix 4: List of ANOVAS for field trials

Variate: % Emergence

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	174.22	87.11	1.35	
Rep.*Units* stratum					
Planting Date	2	11446.22	5723.11	88.97	<.001
Variety	3	1203.56	401.19	6.24	0.003
Planting Date*Variety	6	767.11	127.85	1.99	0.111
Residual	22	1415.11	64.32		
Total	35	15006.22			

Variate: Leaf number

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	2.0889	1.0445	1.83	
Rep.*Units* stratum					
Planting Date	2	270.0779	135.0390	235.97	<.001
Variety	3	2.2855	0.7618	1.33	0.269
DAS	3	306.3088	102.1029	178.42	<.001
Planting Date*Variety	6	8.6844	1.4474	2.53	0.026
Planting Date*DAS	6	12.8535	2.1423	3.74	0.002
Variety*DAS	9	3.7575	0.4175	0.73	0.681
Planting Date*Variety*DAS	18	5.1731	0.2874	0.50	0.951
Residual	94	53.7938	0.5723		
Total	143	665.0234			

Variate: Plant Height (cm)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	1557.6	778.8	7.61	
Rep.*Units* stratum					
Planting Date	2	84919.0	42459.5	415.14	<.001
Variety	3	2636.3	878.8	8.59	<.001
DAS	3	136825.3	45608.4	445.93	<.001
Planting Date*Variety	6	2920.9	486.8	4.76	<.001
Planting Date*DAS	6	22497.0	3749.5	36.66	<.001
Variety*DAS	9	478.2	53.1	0.52	0.857
Planting Date*Variety*DAS	18	881.8	49.0	0.48	0.961
Residual	94	9614.1	102.3		
Total	143	262330.1			

Variate: Tasseling (DAS)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	2.722	1.361	0.19	
Rep.*Units* stratum					
Planting Date	2	9753.722	4876.861	668.02	<.001
Variety	3	49.000	16.333	2.24	0.112
Planting Date*Variety	6	24.500	4.083	0.56	0.758
Residual	22	160.611	7.301		
Total	35	9990.556			

Variate: Ears/plant

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	0.3802	0.1901	0.81	
Rep.*Units* stratum					
Planting Date	2	4.9344	2.4672	10.53	<.001
Variety	3	10.7115	3.5705	15.25	<.001
Planting Date*Variety	6	6.0057	1.0010	4.27	0.005
Residual	22	5.1523	0.2342		
Total	35	27.1842			

Variate: Ear length (cm)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	24.562	12.281	3.49	
Rep.*Units* stratum					
Planting Date	2	18.696	9.348	2.66	0.093
Variety	3	256.030	85.343	24.26	<.001
Planting Date*Variety	6	23.045	3.841	1.09	0.398
Residual	22	77.397	3.518		
Total	35	399.729			

Variate: Ear mass (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	14161.	7080.	2.04	
Rep.*Units* stratum					
Planting Date	2	1469.	734.	0.21	0.811
Variety	3	113289.	37763.	10.88	<.001
Planting Date*Variety	6	19097.	3183.	0.92	0.501
Residual	22	76352.	3471.		
Total	35	224367.			

Variate: Kernel rows/ear

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	15.000	7.500	4.50	
Rep.*Units* stratum					
Planting Date	2	8.172	4.086	2.45	0.109
Variety	3	16.951	5.650	3.39	0.036
Planting Date*Variety	6	7.093	1.182	0.71	0.646
Residual	22	36.665	1.667		
Total	35	83.882			

Variate: Kernel number/ear

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	55943.	27971.	5.69	
Rep.*Units* stratum					
Planting Date	2	66879.	33440.	6.80	0.005
Variety	3	135186.	45062.	9.16	<.001
Planting Date*Variety	6	26870.	4478.	0.91	0.506
Residual	22	108208.	4919.		
Total	35	393086.			

Variate: Grain mass/ear (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	9079.	4539.	2.71	
Rep.*Units* stratum					
Planting Date	2	3782.	1891.	1.13	0.341
Variety	3	55069.	18356.	10.97	<.001
Planting Date*Variety	6	6887.	1148.	0.69	0.663
Residual	22	36810.	1673.		
Total	35	111626.			

Variate: 100 grain mass (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	59.36	29.68	0.96	
Rep.*Units* stratum					
Planting Date	2	484.48	242.24	7.82	0.003
Variety	3	613.84	204.61	6.61	0.002
Planting Date*Variety	6	349.08	58.18	1.88	0.130
Residual	22	681.13	30.96		
Total	35	2187.89			

Variate: Yield (t/ha)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	6.597	3.299	2.78	
Rep.*Units* stratum					
Planting Date	2	2.734	1.367	1.15	0.335
Variety	3	38.389	12.796	10.77	<.001
Planting Date*Variety	6	4.919	0.820	0.69	0.660
Residual	22	26.143	1.188		
Total	35	78.782			

Appendix 5: List of ANOVAs for Hydro-priming Experiment

Variate: Daily Germination (%)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	235.81	117.90	4.01	
Rep.*Units* stratum					
Variety	3	2022.86	674.29	22.92	<.001
Treatment	2	1104.38	552.19	18.77	<.001
Day	6	157372.32	26228.72	891.44	<.001
Variety*Treatment	6	4804.95	800.83	27.22	<.001
Variety*Day	18	1370.03	76.11	2.59	<.001
Treatment*Day	12	16273.40	1356.12	46.09	<.001
Variety*Treatment*Day	36	4519.49	125.54	4.27	<.001
Residual	166	4884.19	29.42		
Total	251	192587.43			

Variate: Final Germination (%)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	46.22	23.11	1.61	
Rep.*Units* stratum					
Variety	3	321.78	107.26	7.46	0.001
Treatment	2	331.56	165.78	11.53	<.001
Variety*Treatment	6	272.89	45.48	3.16	0.022
Residual	22	316.44	14.38		
Total	35	1288.89			

Variate: GVI

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	22.97	11.48	1.14	
Rep.*Units* stratum					
Variety	3	200.38	66.79	6.64	0.002
Treatment	2	704.60	352.30	35.02	<.001
Variety*Treatment	6	422.38	70.40	7.00	<.001
Residual	22	221.30	10.06		
Total	35	1571.62			

Variate: MGT (days)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	0.001667	0.000833	0.16	
Rep.*Units* stratum					
Variety	3	0.021111	0.007037	1.39	0.273
Treatment	2	0.851667	0.425833	83.90	<.001
Variety*Treatment	6	0.203889	0.033981	6.69	<.001
Residual	22	0.111667	0.005076		
Total	35	1.190000			

Variate: Root length (mm)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	9	21262.	2362.	1.66	
Rep.*Units* stratum					
Variety	3	27815.	9272.	6.52	<.001
Treatment	2	440.	220.	0.15	0.857
Variety*Treatment	6	36935.	6156.	4.33	<.001
Residual	99	140867.	1423.		
Total	119	227320.			

Variate: Shoot length (mm)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	9	11503.7	1278.2	4.23	
Rep.*Units* stratum					
Variety	3	2223.6	741.2	2.45	0.068
Treatment	2	12700.9	6350.4	21.02	<.001
Variety*Treatment	6	28272.3	4712.0	15.60	<.001
Residual	99	29906.7	302.1		
Total	119	84607.2			

Variate: Root:shoot

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	9	1.5458	0.1718	1.67	
Rep.*Units* stratum					
Variety	3	1.3624	0.4541	4.41	0.006
Treatment	2	1.3217	0.6608	6.42	0.002
Variety*Treatment	6	1.5408	0.2568	2.49	0.027
Residual	99	10.1910	0.1029		
Total	119	15.9618			

Variate: Fresh Weight (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	9	0.67907	0.07545	1.50	
Rep.*Units* stratum					
Variety	3	0.21715	0.07238	1.44	0.235
Treatment	2	1.21752	0.60876	12.13	<.001
Variety*Treatment	6	1.83075	0.30512	6.08	<.001
Residual	99	4.96815	0.05018		
Total	119	8.91264			

Variate: Dry Mass (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	9	0.023430	0.002603	0.68	
Rep.*Units* stratum					
Variety	3	0.193853	0.064618	16.80	<.001
Treatment	2	0.035082	0.017541	4.56	0.013
Variety*Treatment	6	0.062652	0.010442	2.72	0.017
Residual	99	0.380730	0.003846		
Total	119	0.695747			

Variate: Final Emergence (%)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	100.00	50.00	2.23	
Rep.*Units* stratum					
Variety	3	159.72	53.24	2.37	0.083
Treatment	2	8.33	4.17	0.19	0.831
FC	1	12.50	12.50	0.56	0.459
Variety*Treatment	6	136.11	22.69	1.01	0.431
Variety*F.Capacity	3	15.28	5.09	0.23	0.877
Treatment*F.Capacity	2	108.33	54.17	2.41	0.101
Variety*Treatment*F.Capacity	6	13.89	2.31	0.10	0.996
Residual	46	1033.33	22.46		
Total	71	1587.50			

Variate: Daily Emergence (%)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	566.87	283.43	4.26	
Rep.*Units* stratum					
Variety	3	5315.38	1771.79	26.64	<.001
Treatment	2	16193.65	8096.83	121.73	<.001
FC	1	52433.43	52433.43	788.27	<.001

Day	13	1610782.64	123906.36	1862.77	<.001
Variety*Treatment	6	3820.63	636.77	9.57	<.001
Variety*F.Capacity	3	2955.85	985.28	14.81	<.001
Treatment*F.Capacity	2	26753.17	13376.59	201.10	<.001
Variety*Day	39	6619.35	169.73	2.55	<.001
Treatment*Day	26	54273.02	2087.42	31.38	<.001
F.Capacity*Day	13	73376.29	5644.33	84.86	<.001
Variety*Treatment*F.Capacity	6	1042.06	173.68	2.61	0.017
Variety*Treatment*Day	78	6090.48	78.08	1.17	0.156
Variety*F.Capacity*Day	39	4084.42	104.73	1.57	0.016
Treatment*F.Capacity*Day	26	40224.60	1547.10	23.26	<.001
Variety*Treatment*F.Capacity*Day	78	4846.83	62.14	0.93	0.638
Residual	670	44566.47	66.52		
Total	1007	1953945.14			

Variate: MET(days)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	0.06591	0.03296	0.48	
Rep.*Units* stratum					
Variety	3	0.64293	0.21431	3.15	0.034
Treatment	2	4.83383	2.41691	35.56	<.001
FC	1	14.56047	14.56047	214.24	<.001
Variety*Treatment	6	0.68322	0.11387	1.68	0.149
Variety*F.Capacity	3	0.48966	0.16322	2.40	0.080
Treatment*F.Capacity	2	6.70665	3.35333	49.34	<.001
Variety*Treatment*F.Capacity	6	0.43693	0.07282	1.07	0.393
Residual	46	3.12634	0.06796		
Total	71	31.54594			

Variate: Plant Height (mm)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	11781.3	5890.6	9.20	
Rep.*Units* stratum					
Variety	3	9363.1	3121.0	4.87	0.003
Treatment	2	24983.6	12491.8	19.51	<.001
FC	1	56680.6	56680.6	88.51	<.001
Week	2	1153857.9	576929.0	900.94	<.001
Variety*Treatment	6	9875.3	1645.9	2.57	0.022
Variety*F.Capacity	3	7536.4	2512.1	3.92	0.010
Treatment*F.Capacity	2	2348.2	1174.1	1.83	0.164
Variety*Week	6	8011.1	1335.2	2.09	0.059
Treatment*Week	4	28691.5	7172.9	11.20	<.001
F.Capacity*Week	2	8517.5	4258.7	6.65	0.002
Variety*Treatment*F.Capacity	6	8819.6	1469.9	2.30	0.038
Variety*Treatment*Week	12	5145.6	428.8	0.67	0.778
Variety*F.Capacity*Week	6	2419.6	403.3	0.63	0.706
Treatment*F.Capacity*Week	4	2590.3	647.6	1.01	0.404

Variety*Treatment*F.Capacity*Week	12	5295.7	441.3	0.69	0.760
Residual	142	90932.0	640.4		
Total	215	1436849.3			

Variate: Leaf No.

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	3.1204	1.5602	6.35	
Rep.*Units* stratum					
Variety	3	0.0926	0.0309	0.13	0.945
Treatment	2	6.5093	3.2546	13.25	<.001
FC	1	21.4074	21.4074	87.15	<.001
Week	2	147.2870	73.6435	299.81	<.001
Variety*Treatment	6	0.8241	0.1373	0.56	0.762
Variety*F.Capacity	3	1.1481	0.3827	1.56	0.202
Treatment*F.Capacity	2	2.6759	1.3380	5.45	0.005
Variety*Week	6	0.4907	0.0818	0.33	0.919
Treatment*Week	4	3.2685	0.8171	3.33	0.012
F.Capacity*Week	2	0.1759	0.0880	0.36	0.700
Variety*Treatment*F.Capacity	6	3.1019	0.5170	2.10	0.056
Variety*Treatment*Week	12	1.5093	0.1258	0.51	0.904
Variety*F.Capacity*Week	6	1.6019	0.2670	1.09	0.373
Treatment*F.Capacity*Week	4	2.4907	0.6227	2.54	0.043
Variety*Treatment*F.Capacity*Week	12	1.3981	0.1165	0.47	0.927
Residual	142	34.8796	0.2456		
Total	215	231.9815			

Variate: Root length (mm)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	286.36	143.18	2.62	
Rep.*Units* stratum					
Variety	3	155.17	51.72	0.95	0.427
Treatment	2	482.03	241.01	4.40	0.018
FC	1	227.56	227.56	4.16	0.047
Variety*Treatment	6	795.42	132.57	2.42	0.041
Variety*F.Capacity	3	232.33	77.44	1.41	0.250
Treatment*F.Capacity	2	465.03	232.51	4.25	0.020
Variety*Treatment*F.Capacity	6	262.42	43.74	0.80	0.576
Residual	46	2517.64	54.73		
Total	71	5423.94			

Variate: Shoot length (mm)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	4401.	2201.	1.81	
Rep.*Units* stratum					
Variety	3	20604.	6868.	5.66	0.002
Treatment	2	27658.	13829.	11.40	<.001
FC	1	18883.	18883.	15.57	<.001
Variety*Treatment	6	18806.	3134.	2.58	0.031
Variety*F.Capacity	3	2587.	862.	0.71	0.550
Treatment*F.Capacity	2	3891.	1945.	1.60	0.212
Variety*Treatment*F.Capacity	6	13234.	2206.	1.82	0.116
Residual	46	55797.	1213.		
Total	71	165861.			

Variate: Root:Shoot

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	0.002603	0.001302	0.30	
Rep.*Units* stratum					
Variety	3	0.015817	0.005272	1.22	0.313
Treatment	2	0.013752	0.006876	1.59	0.214
FC	1	0.011557	0.011557	2.68	0.109
Variety*Treatment	6	0.036572	0.006095	1.41	0.231
Variety*F.Capacity	3	0.007333	0.002444	0.57	0.640
Treatment*F.Capacity	2	0.009681	0.004840	1.12	0.335
Variety*Treatment*F.Capacity	6	0.042652	0.007109	1.65	0.156
Residual	46	0.198572	0.004317		
Total	71	0.338539			

Variate: Root Fresh Weight (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	0.08694	0.04347	0.77	
Rep.*Units* stratum					
Variety	3	1.02556	0.34185	6.03	0.001
Treatment	2	0.30528	0.15264	2.69	0.078
FC	1	0.37556	0.37556	6.63	0.013
Variety*Treatment	6	0.84028	0.14005	2.47	0.037
Variety*F.Capacity	3	0.08778	0.02926	0.52	0.673
Treatment*F.Capacity	2	0.00361	0.00181	0.03	0.969
Variety*Treatment*F.Capacity	6	0.15972	0.02662	0.47	0.827
Residual	46	2.60639	0.05666		
Total	71	5.49111			

Variate: Shoot Fresh Weight (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	0.05861	0.02931	0.32	
Rep.*Units* stratum					
Variety	3	0.84500	0.28167	3.06	0.037
Treatment	2	3.31444	1.65722	18.00	<.001
FC	1	0.98000	0.98000	10.65	0.002
Variety*Treatment	6	0.73667	0.12278	1.33	0.262
Variety*F.Capacity	3	0.39444	0.13148	1.43	0.247
Treatment*F.Capacity	2	0.30333	0.15167	1.65	0.204
Variety*Treatment*F.Capacity	6	0.44556	0.07426	0.81	0.570
Residual	46	4.23472	0.09206		
Total	71	11.31278			

Variate: Root Dry Mass (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	0.025103	0.012551	3.89	
Rep.*Units* stratum					
Variety	3	0.141193	0.047064	14.59	<.001
Treatment	2	0.000544	0.000272	0.08	0.919
FC	1	0.005513	0.005513	1.71	0.198
Variety*Treatment	6	0.029544	0.004924	1.53	0.191
Variety*F.Capacity	3	0.015082	0.005027	1.56	0.212
Treatment*F.Capacity	2	0.001433	0.000717	0.22	0.802
Variety*Treatment*F.Capacity	6	0.032789	0.005465	1.69	0.144
Residual	46	0.148431	0.003227		
Total	71	0.399632			

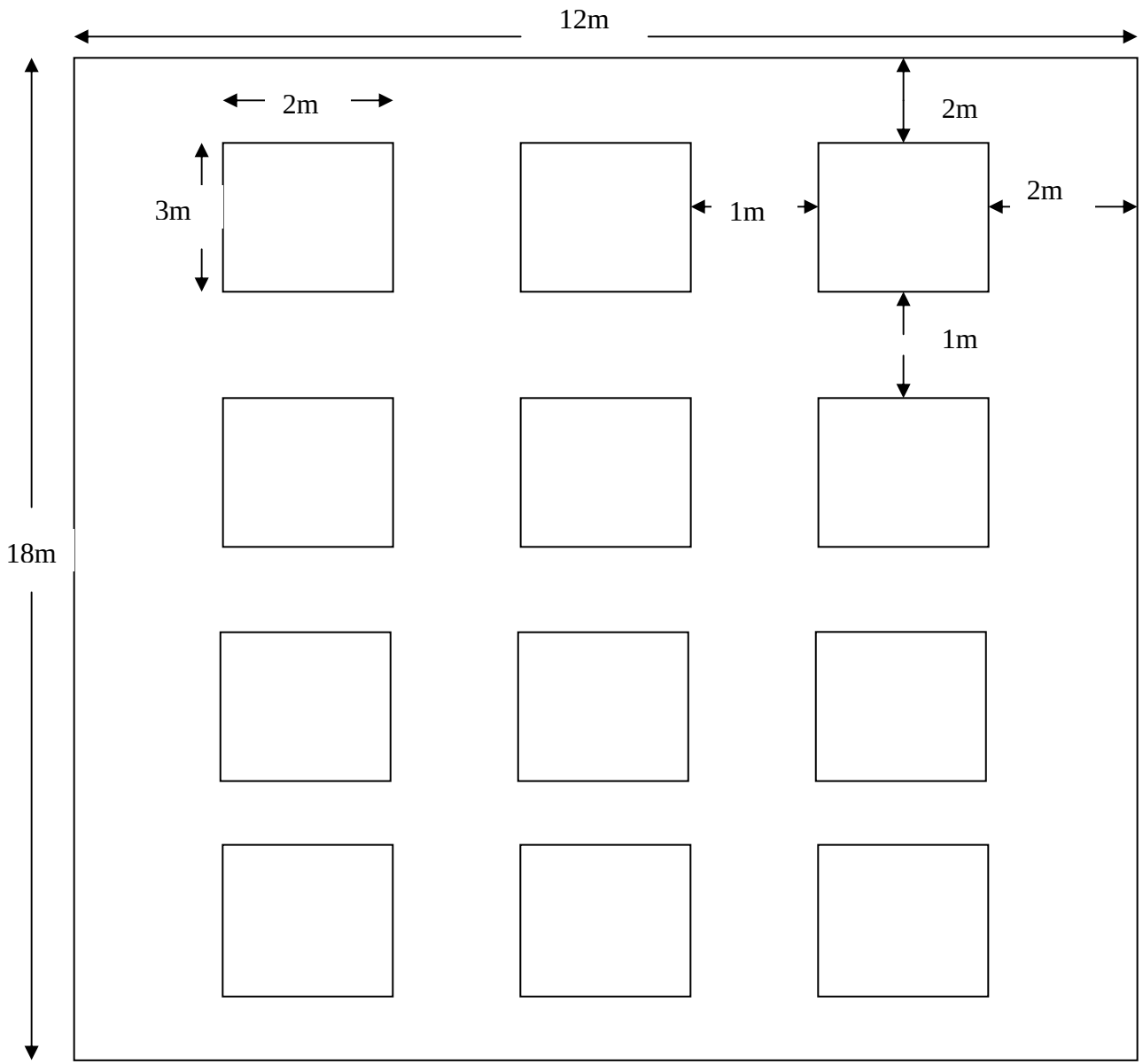
Variate: Shoot Dry Mass (g)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	0.000758	0.000379	0.20	
Rep.*Units* stratum					
Variety	3	0.004760	0.001587	0.83	0.483
Treatment	2	0.022433	0.011217	5.88	0.005
FC	1	0.014735	0.014735	7.72	0.008
Variety*Treatment	6	0.014411	0.002402	1.26	0.295
Variety*F.Capacity	3	0.004693	0.001564	0.82	0.490
Treatment*F.Capacity	2	0.004478	0.002239	1.17	0.318
Variety*Treatment*F.Capacity	6	0.007144	0.001191	0.62	0.710
Residual	46	0.087775	0.001908		
Total	71	0.161188			

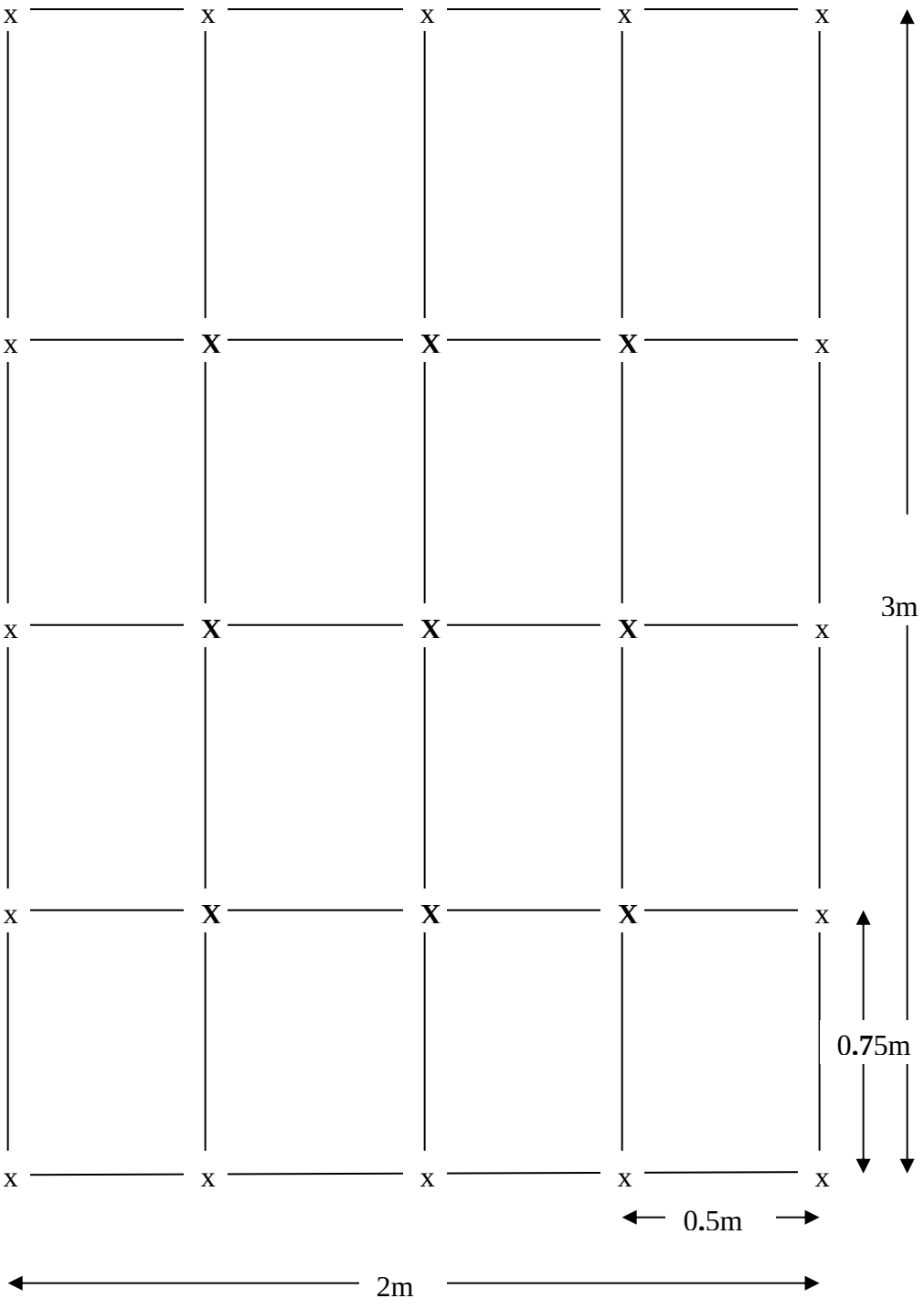
Variate: Leaf area (cm^2)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	44.5	22.2	0.14	
Rep.*Units* stratum					
Variety	3	1975.8	658.6	4.16	0.011
Treatment	2	2579.7	1289.9	8.15	<.001
FC	1	2978.4	2978.4	18.81	<.001
Variety*Treatment	6	1240.4	206.7	1.31	0.274
Variety*F.Capacity	3	956.4	318.8	2.01	0.125
Treatment*F.Capacity	2	171.1	85.5	0.54	0.586
Variety*Treatment*F.Capacity	6	1201.5	200.3	1.27	0.292
Residual	46	7281.9	158.3		
Total	71	18429.7			

Appendix 6: Field Trial Layouts



Individual Plot Layout



Key:

x= non-experimental plant

X= experimental plant

Appendix 7: Proline Standard Curve