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DISSERTATION

PHYSIOLOGICAL ASPECTS OF DROUGHT TOLERANCE IN WINTER WHEAT

Submitted by
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In Partial fulfillment of the requirements
for the Degree of Doctor of Philosophy
Colorado State University
Fort Collins, Colorado
Fall 2000

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY QASIM A. KHAN ENTITLED PHYSIOLOGICAL ASPECTS OF DROUGHT TOLERANCE IN WINTER WHEAT BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Duane L. Johnson

Advisor

Department Head

ABSTRACT OF DISSERTATATION

PHYSIOLOGICAL ASPECTS OF DROUGHT TOLERANCE IN WINTER WHEAT

Limited moisture availability due to low precipitation is a major constraint in winter wheat production throughout the Central Great Plains of the USA. Water stress at flowering or during grain filling is a characteristic of the environment of this region and other parts of the world where wheat is grown. Several experiments were conducted in the field and greenhouse both under well watered and water stress conditions. The objectives of this study were to (i) assess the usefulness of a chemical desiccant ($NaClO_3$); (ii) evaluate water relations, canopy temperature depression (CTD), and chlorophyll content in selecting genotypes under drought stress and (iii) estimate the heritability of water potential (Ψ) and relative water content (RWC) by parent-offspring regression and parent-offspring correlations using F_4 plants and their F_5 progeny means.

The responses of nine cultivars to chemical desiccant, applied 10 days postanthesis, indicated that cultivars with heavier kernels generally suffered lower desiccation injuries (grain yield and kernel weight injury). There was no association between the drought stress and desiccant stress in the field; however, the chemical desiccant effects were more repeatable than drought because the fluctuations caused by natural environmental conditions were greatly reduced. The use of a chemical desiccant in the greenhouse is not recommended because the ranking of some cultivars (for grain yield and kernel weight injury) was different than in the field. The application of the chemical desiccation method to early generation bulk populations did not consistently differentiate among the crosses. The chemical desiccation injury was much higher in the F_4 generation than F_3 generation, possibly due to the deleterious effect of the desiccant on grain growth.

Cultivar differences were detected for Ψ, RWC, CTD, and chlorophyll content. Significant genetic variability was detected in the F_4 and F_5 generations among crosses for Ψ and RWC. The cross Sandy/TAM 107 consistently exhibited higher Ψ and RWC than Sandy/Yuma, and Sandy/Lamar crosses. Parent-offspring regressions and parent-offspring correlations were generally low for Ψ and RWC; however, Sandy/TAM 107 showed higher heritability both for Ψ (0.27 - 0.68) and RWC (0.45 - 0.59). In the unselected early-generation bulk populations, the crosses showed significant differences for RWC, while the crosses were the same for Ψ. Thus, the progeny selection method would be more beneficial than the bulk selection method for Ψ. The challenge is to use these traits for selection in actual breeding programs that will lead to superior performance of wheat genotypes in dry environments.

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DEDICATION

To my parents, for their never-ending love and who always pray for my success in every field of life,

To Bagas, for her love, support, endurance and belief in me,

To Hammad and Isbah, for brightening my life.

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CHAPTER I

LITERATURE REVIEW

Water stress and crop growth

As a meteorological term, drought means a lack of precipitation over a prolonged period of time. In an agriculture context, drought exists when the amount and distribution of precipitation are sufficiently low to cause serious reduction in the crop yield (Hale and Orcult, 1989). In general, water deficit occurs in plants whenever atmospheric demand exceeds the supply of water from the soil. Water stress in plants develops as a consequence of water loss from the leaf as the stomata open to allow the exchange of CO_2 gas for photosynthesis (Turner, 1986).

The water status of plants is usually defined in terms of water potential (Ψ) and its components. Scholander et al. (1965) developed a satisfactory and simple pressure bomb method, which provides an easy way to measure Ψ in plants. In general, Ψ is considered to be a total of osmotic potential (Ψ_s), pressure potential (Ψ_p), and matrix potential (Ψ_m): $\Psi = \Psi_s + \Psi_p + \Psi_m$. As osmotic potential and metric potential are defined to be negative, pressure potential is positive, and the total Ψ, is negative as it describes the free energy of water in the system related to pure water (Salisbury and Ross, 1985). According to Ehrler et al. (1978) and Schonfeld et al. (1988) in plant tissue Ψ_m is considered to be small and usually ignored. Therefore, in plants $\Psi = \Psi_s + \Psi_p$.

Another commonly used indicator of plant water status is Relative Water Content (RWC). RWC is the water content (on a percentage basis) relative to water content of the same tissue at full turgor (after floating on water to "constant" weight). RWC is related to the water potential of the same tissue; however, this association depends on the species and growth stage of the plants (Hsiao, 1973). Sinclair and Ludlow (1985) suggested that RWC is a better indicator of water stress in plant tissue than water potential. In wheat, water potential ranges from -0.5 to -1.6 Mpa, with slight differences among tissues, under well-watered conditions. However, under field conditions, leaf water potentials of -2.0 to -3.5 Mpa are common. Drought markedly reduces water content of leaves and stems, but has little effect on water content of the grains.

Drought stress results in plant water deficits that, among other things, lead directly to changes in the physical environment of the crops; these changes may subsequently affect crop physiology (Day, 1981). At the onset of drought, water is lost from the soil causing a decrease in soil water potential and soil hydraulic conductivity. Thus, it becomes more difficult for plants to extract water (Gardner, 1960). As a result, plant Ψ and leaf water content tends to decline, causing a reduction in cell turgor pressure. Loss of turgor can cause leaves to wilt, thus decreasing the light interception and reducing photosynthesis rate. Leaf surface is reduced in water-stressed plants from reduction in cell expansion, and also stress-induced leaf shedding. With severe stress, the photosynthetic machinery may be damaged, leading to a reduction in the rate of photosynthesis per unit leaf area. Continual stress affects many other physiological processes, and eventually results in cessation of growth (Idso et al., 1977; Blum, 1988).

Indirect effects of water stress on crop growth may occur through the action of plant hormones. Root exposure to drying topsoil may cause induction of root hormonal signal to the shoot that cause a reduction in plant assimilation and growth (Davies et al., 1994). There is increasing evidence that plants may react to a drying top soil well before their leaves wilt and even before there is a detectable change in water potential of the leaves. Drought causes an increase in abscisic acid (ABA) in many higher crop plants including wheat; its concentration in leaves increases during water stress causing stomatal closure, reduction in assimilate, and reproductive failure (Trewavas and Jones, 1991). These physical, physiological, and chemical effects of water stress depend on the degree and the timing of drought conditions in relation to the stage of plant development (Hale and Orcult, 1989).

Drought resistance mechanisms

Drought resistance is the ability of a plant to live, grow and yield satisfactorily with limited water supply or under periodic water stress (Levitt, 1980; Gupta and O'Toole, 1986). For plants living in natural habitats, survival of drought conditions is probably more important than high productivity, whereas in agricultural systems, maximization of productivity is of prime importance. Levitt (1980) categorized drought resistance into drought avoidance and drought tolerance. He stated that drought-avoiding plants maintain high internal water potential, in spite of low environmental water availability. To plant breeders, drought resistance is the ability of one genotype to be more productive with a given amount of soil water than another (Quizenberry, 1981). Plant survival and production under drought can occur through different mechanisms. These mechanisms are generally classified into the following categories (Gupta and O'Toole, 1986):

a: Drought escape is the ability of a plant to mature before water stress becomes a serious limiting factor. Drought escape is usually associated with early maturity to avoid onset of severe water deficits.

b: Drought avoidance is the ability of a plant, through various morphological and physiological adaptations, to maintain high water status during a drought. Some important traits associated with drought avoidance mechanisms are: increased root density (Sanchez and Kramer, 1971); leaf water retention (Clark and McCaig, 1982), reduced leaf conductance (Fischer and Sanchez, 1979); epicuticular wax (O'Toole, 1982); reduced leaf area (Turner and Begg, 1981); leaf rolling and tolerance to high crop canopy temperature (Blum, 1982).

c: Drought tolerance is the ability of a plant, through various morphological and physiological responses, to withstand water deficit as measured by degree and duration of low plant water potential. Drought tolerance mechanisms includes osmotic adjustment (Morgan, 1983); translocation of assimilates (Blum et al., 1983a) and membrane stability (Blum, 1988).

d: Finally, drought recovery is the ability of a plant to resume growth after drought stress, with a minimum of irreversible yield loss. Recovery mechanisms can be achieved by features such as a shallow root system, by rapid water uptake as soon as rainfalls after drought, or hypersensitivity where plant tissues react by entering a dormant stage as water deficit occurs and immediately recovering when water becomes available again (Baker, 1989).

Drought resistance may be conferred on plants by any one or a combination of the above four mechanisms. A detailed review of drought resistance can be found in (Baker, 1989; Blum, 1988; Levitt, 1980; Turner, 1986).

Plant response to water stress

When stress develops rather gradually in plants the change is likely a slowing down of shoot and leaf growth (Hsiao, 1973). Leaves are the primary plant site of carbon fixation, synthesis of nitrogenous compounds, and transpiration. Since leaf growth is particularly sensitive to water deficits, drought stress has a significant effect on physiological and biochemical processes. Drought adversely affects the canopy area development through its negative effect on leaf initiation or senescence of leaves already present (Simmons, 1987). Drought inhibits tiller initiation or growth, which leads to a potential loss of seed yield in non-forage cereals (Simpson, 1981). Drought reduces tiller size and number in wheat (Stark and Langley, 1986, Blum et al., 1990). The tillering process is a major determinant of grain yield in wheat (Hucl and Baker, 1989).

Root growth is strongly influenced by moisture availability. Root activity is often reduced indirectly through stress induced growth inhibition, and thus the effect on nutrient uptake may be observed. Improvement of the wheat root system has lagged behind than that of above-ground plant characteristics because of the time consuming nature of root measurement and the variability inherent in different climatic edaphic situations (Rosiella et al., 1993).

Several comprehensive reviews on the physiological responses to water deficits have been published in recent years (Hsiao, 1973; Turner, 1986; Blum, 1988), including two recent reviews by Ludlow and Muchow (1990) and Loss and Siddique (1994).

The effect of drought stress on physiological processes that affect grain yield can be examined in term of their effects on stomatal behavior, photosynthesis, respiration and photorespiration, and translocation of assimilates (Begg and Turner, 1976).

Water stress results in a decrease in transpiration due to stomatal closure (Hsiao, 1973). Stomata close in response to a critical threshold level of leaf water potential and RWC. Stomatal closure occurs over a narrow range of leaf water potential and results in a 20 to 30 fold increase in leaf resistance. Stomata are able to both sense the aerial environment and close under conditions that might otherwise lead to water deficits, and respond to internal turgor losses induced by abscisic acid (Hay and Walker, 1989). Since the stomatal aperture regulates the influx of CO_2 into the leaf as well as loss of water from the leaf, water deficits sufficient to close stomata, also reduce photosynthesis

(Begg and Turner, 1976). This has often been referred to as a stomatal limitation to photosynthesis. However a nonstomatal limitation has also received considerable attention. Nonstomatal effects considered particularly related with the biochemical apparatus involved in carbon assimilation (inhibition of Calvin cycle enzymes such as RuBP carboxylase, and enhanced photorespiration). Nonstomatal effects are thought to become more important than stomatal limitation under severe drought stress conditions. Water stress reduced net photosynthesis in the flag leaf, top internode and ear of wheat (Wardlaw, 1967). Decline in photosynthesis is both by reduction in total photosynthetic area and by reduction in the rate of photosynthesis per unit area.

Respiration and photorespiration are also affected by water stress, usually reduced with increased level of water stress (Hay and Walker, 1989). The decrease in photorespiration in response to increasing drought stress is less than the gross photosynthesis; thus, the ratio of photorespiration to gross photosynthesis increases with increasing level of water stress. Along with the inhibitory effect of Calvin cycle enzymes, the increase in photorespiration relative to gross photosynthesis leads to decreased photosynthetic efficiency and a greater nonstomatal limitation to photosynthesis (Hay and Walker, 1989).

Grain growth in wheat depends on carbon from three main sources: current assimilation, remobilization of pre-anthesis assimilates stored in the stem and other parts, and retranslocation of assimilates stored temporarily in the stem after anthesis (Kobata et al., 1992). About 70% to more than 90% of the grain yield is derived from photoassimilate after anthesis (Austin et al., 1977). Wheat grown under drought may depend more on reserve assimilates for grain filling as photosynthesis after anthesis tends to decline rapidly. Wardlaw (1967) studied photosynthesis under water stress and related effects on carbohydrate translocation and grain growth. He found that water stress induced reduction in flag leaf photosynthesis was not the result of either a failure to utilize assimilates or a failure to move assimilates through conducting tissue. The effect of water stress was to delay and reduce the transfer of sugars from the assimilating tissue to the conducting tissues, not on inhibition of translocation within the conducting tissues themselves.

Stem reserves and grain growth

In cereals, grain growth is partially supported by translocated plant reserves stored mainly in the stem prior to anthesis. Grain yield of cereals is governed by the rate and duration of grain filling. Stems of wheat and other cereals accumulate nonstructural carbohydrates (NSCs) in the form of glucose, fructose, sucrose, and starch near anthesis, and by maturity they have nearly disappeared (McCaig and Clark, 1982). Fructans, the most important stem NSC component, increase throughout stem development and account for up to two-thirds of total NSC and about one-third of the stem dry weight at anthesis (McCaig and Clark, 1982; Hendrix et al., 1986). Fructans accumulate in the internodes, mostly in the top two internodes during extension (Wardlaw and Porter, 1967), although most of the fructans in internodes accumulate after it is fully extended. Assimilate availability, particularly carbohydrate, strongly influence grain filling. Assimilation and partitioning of photosynthate in relation to grain growth are, therefore, of prime importance (Wardlaw and Porter, 1967; Rawson and Evans, 1971; Austin et al., 1977). Assimilate supply for grain growth comes primarily from photosynthesis after anthesis, and NSCs assimilated near anthesis are temporarily stored before being moved to the grain (Gallagher et al., 1976). Wardlaw and Porter (1967) reported that NSCs stored in the stem before anthesis were distributed to developing grains and for the most part, not lost in respiration.

The lag phase (between the termination of stem growth and the initiation of kernel growth) determines the rate of remobilization of NSC from stem to the ear (Rawson and Evans, 1971; Hunt, 1979). The temporary storage of NSCs in the wheat stem acts to correct the phase difference between the time of maximum photosynthate production by the plant and the time of maximum requirement for carbohydrate by the developing grain (McCaig and Clark, 1982). Environmental conditions that decrease current assimilation during grain filling cause a greater demand for stem reserves for grain filling. In the absence of stress, the amount of storage appears to be unrelated to grain yield (Rawson and Evans, 1971; Hossain et al., 1990); however, there is good evidence to suggest that temporary storage is very important under stress conditions (Bidinger et al., 1977; Aggarwal and Sinha, 1984). Gallagher et al. (1976) studied grain growth patterns of field-grown winter wheat under drought stressed and nonstressed conditions. In their study, the contribution of translocated material assimilated before anthesis to final grain weight was greater when conditions during grain filling were adverse for photosynthesis. Pheloung and Siddique (1991) found that NSC contribution to grain filling was greater under dry conditions than under irrigated conditions. Aggarwal and Sinha (1984) reported that a drought tolerant cultivar mobilized greater amount of NSC than a drought susceptible cultivar and that contribution of NSC was greater for both cultivars under non-irrigated than under irrigated conditions.

The mobilization of stem reserves were not only affected by water stress but the rate of development of water deficit is also important. Palta et al. (1994) reported that post anthesis assimilation with a rapid water deficit rate was reduced by 57% relative to a slow rate. Remobilization of reserves increased 36%, while total grain carbon was reduced by 24%. Several reports have addressed the relative NSC contribution to grain filling under conditions adverse to current photosynthesis (Austin et al., 1980; Pheloung and Siddique, 1991; Palta et al., 1994).

Stem length is important in affecting stem reserve storage. Fischer and Stockman (1986) reported that dwarfing genes increased the weight of spike tissue at anthesis as a proportion of the total above ground weight. Pheloung and Siddique (1991) found that under dry conditions a modern semidwarf cultivar utilized more stem NSCs than a modern, tall cultivar. Austin et al. (1977), using the derivatives of barley crosses between single-dwarf parents containing different, nonallelic dwarfing genes, reported that the differences among the lines in the relative NSC contribution to grain filling were not attributable to difference in plant height.

Estimates of relative contribution of stored NSCs to the total grain weight per ear or to grain yield varied depending on the experimental conditions and cultivars used. These contributions were estimated to be anywhere between 6 to 100 percent (Blum, 1998).

Studies on other crops, by Austin et al. (1977) with barley, Muchow (1990) with sorghum and Hall et al. (1990) with sunflower have provided additional evidence that NSC contribution to grain filling may be greater under postanthesis conditions that limit current photosynthesis.

Methods of drought resistance

Although numerous plant mechanisms have been proposed in an attempt to describe the physiological response of plant to water stress, few of these mechanisms have been successfully related to plant production and yield in the field (Blum et al., 1982). Before suitable screening techniques can be developed for identifying germplasm adapted to drought prone areas, a better understanding of the physiological response of the plant to water stress is needed. Future yield improvements may be hasten by a better understanding of factors that control growth, development, and yield of cereals (Shorter et al., 1991).

Development of plant cultivars and genotypes tolerant to drought stress is an objective in many breeding programs. Genetic improvement of drought resistance in crop plants requires identification of relevant physiological stress tolerance mechanisms as selection criteria (Blum, 1988). Success in breeding to improve drought resistance of crop cultivars has been limited by lack of appropriate strategies and screening techniques (Blum et al., 1981) and a lack of knowledge of what determines stress resistance in crop plants (Moss et al., 1974). For a screening technique to be effective it should not only correlate well with critical physiological processes, but also be rapid, simple, accurate, nondestructive (Simpson, 1981) and applicable to many plant developmental stages and tissues (Sullivan, 1972).

Several techniques have been developed to screen for drought resistance; for example, excised leaf water retention (Clark and McCaig, 1982), epicuticular waxes (Johnson et al., 1983) stomatal number (Kazemi et al., 1978), stomatal conductance (Jones, 1977), canopy temperature (Blum et al., 1982), osmotic adjustment (Morgan, 1983), chemical desiccation (Blum, 1983a), leaf water potential (Scholander et al., 1965) and RWC (Barrs, 1968).

Osmotic adjustment is a decrease in cell osmotic potential due to the accumulation of solutes rather than to a decrease in cellular volume (Turner and Jones, 1980). This help to maintain turgor as plant experience water stress and allows turgor driven processes as water deficits develop in plants at lower water potentials (Turner, 1986; Morgan, 1983). Morgan and Condon (1986) showed that under limited water supply, plants with higher osmoregulation produce more root biomass and extract more soil water and produce more dry matter and maintained harvest index in wheat. Morgan et al. (1993) found little differences in osmoregulation among wheat genotypes when they were tested in the field.

Plant water potential has been found to be a reliable measurement of the water status of plant tissues. Great progress towards the ability to determined crop water status was made after the development of pressure chamber for water potential measurement (Scholander et al., 1965). Its portability and suitability for field conditions led to its adoption by many research programs. Leaf Ψ is a useful measurement in determining the relative extent of water deficits in plant tissues. High leaf Ψ during water stress can be maintained through reduction of water loss by various morph-physiological mechanisms e.g.; stomatal resistance (Blum et al., 1981); reduction in leaf area; increased epicuticular waxes (Johnson et al., 1983); leaf rolling and also by rooting depth (Turner, 1986). When water stress cause reduction in Ψ the mechanisms that permit plant to maintain turgor at lower water potential to continue growth and metabolic processes are of use. One such mechanism is osmotic adjustment that was discussed earlier. High grain yield is associated with low leaf Ψ because it maintained the green leaf tissues which enabled high yielding cultivars to tolerate water stress (Winter et al., 1988). Martin et al. (1993) while working with wheat concluded that the adaptability of cultivar Sandy (a drought tolerant cultivar) to water limiting environment may be due to its low leaf Ψ maintenance which, in turn, is related to high osmotic adjustment in response to water stress. Many workers have suggested that total Ψ of plant tissue may be useful in selecting drought resistant cultivars of wheat (Blum, 1998; Winter et al., 1988;). Blum and Sullivan (1997) and Kirkham et al. (1978) found that shorter cultivars maintained higher leaf Ψ than taller cultivars.

The water status in plants can also be measured as *relative water content* using a simple technique based on turgid and dry weight of plant tissue (Barrs, 1968). Schonfeld et al. (1988) in evaluating the RWC of wheat cultivars under stress environment indicated that cultivars with higher RWC are more drought resistant. In a comparison between a drought resistant (TAM 101) and a drought susceptible (Sturdy) cultivar, Steven et al. (1990) determined that leaf RWC and apparent photosynthesis were maintained significantly higher by TAM W-101, compared with sturdy, under moderate to severe drought stress.

Sinclair and Ludlow (1985) suggested that leaf RWC is a better indicator of plant water status than water potential. There is still disagreement whether the RWC or leaf Ψ has the greater effect on physiological activity and on survival of plant. Recently, Morgan et al. (1993) found RWC to be a better predictor of stress-induced variation in photosynthesis than leaf Ψ.

Infrared thermometry (IRT) has become widely used to assess plants water status. First proposed by Tanner (1963) it has been used to study the association between plant or canopy temperature and plant water status. The technique is based on the principle of leaf to air temperature differential arising due to varying degrees of stomatal opening or sensitivities.

Three useful methods of remote sensing are used for characterizing plant water status, namely canopy temperature (Tc), canopy-air temperature differential (Tc-Ta), and crop water stress index (Blum, 1988). Leaf canopy temperatures were found to be a reliable indicator of plant water status which in turn is a primary determinant of grain yield (Jackson et al., 1981). Blum et al. (1982) found significant variation in canopy temperature among wheat genotypes when measured with IR thermometer. They demonstrated that as plant Ψ declined, canopy temperatures increased and that lower canopy temperatures were indicative of higher Ψ. A significant association between canopy temperatures and leaf Ψ across wheat genotypes suggests that infrared thermal sensing of canopy temperatures is a valuable screening method for selecting dehydration avoidant cultivars.

Some technical limitations with this technique exist, for example, wind and incomplete canopy cover can cause unreliable measurements. However, a large number of genotypes can be screened in a short period of time, thus this technique has received considerable attention from various workers (Turner and Nicolas, 1987).

The chemical desiccation method is one of the fastest methods to screen genetic material under postanthesis drought stress. Blum et al. (1983a,b) proposed the use of a chemical desiccant as a screen for genetic materials that can support grain growth from stored stem NSCs in the absence of photosynthesis. The treatment does not simulate drought stress, but the effect of stress by inhibiting current assimilation. Magnesium chlorate was applied as a spray to the wheat canopies 14 days postanthesis, inducing complete elimination of the photosynthetic source within two days. Stem and kernel sampling during grain filling showed that reductions occurred in both the rate and duration of grain filling, and that most of the losses in the stem dry weight following desiccation were associated with compensatory increase in kernel growth rate and reductions in kernel weight injury in response to the desiccant.

Beside magnesium chlorate, other chemicals such as sodium chlorate (Hossain et al., 1990; Haley and Quick, 1993) and potassium iodide (Nicolas and

Turner, 1992) were also used to simulate drought stress in wheat. A significantly high association was found between the rate of reduction in kernel weight by chemical desiccation and the rate of reduction by drought stress across divergent genetic materials. The correlation was $r = 0.81^{***}$ and $r = 0.79^{**}$ over two years in Blum (1983b) and $r = 0.48^{**}$ and $r = 0.81^{**}$ over two years in Nicolas and Turner (1992). Hossain et al. (1990) while working on a collection of Great Plains winter wheats reported that desiccated plants retained more NSCs (as a fraction of stem dry weight) in their plant parts than did control plants and that dry matter and carbohydrate losses from the stem of desiccated plants were not strongly associated with yield or kernel weight injury. They also noted that cultivars of stable kernel weight over years and locations sustained relatively less reduction in kernel weight under chemical desiccation.

Selection for larger grains in a breeding population treated with chemical desiccant effectively increase grain yield under postanthesis drought stress with no change in the phenology or plant height, whereas selection without the chemical desiccation treatment did not improve grain filling under postanthesis stress (Blum et al., 1991). Haley and Quick (1993) conducted a similar selection program under chemical desiccation in winter wheat to identify crosses that were tolerant of chemical desiccation. Two cycles of selection produced F_4 bulks that were more resistant to chemical desiccation stress.

Chemical desiccants are more convenient to apply to genotypes of similar maturity, otherwise the desiccant has to be applied to each genotype after they reach anthesis.

Drought resistance traits and grain yield

1. Yield and yield components

Grain yield improvement is the most important objective in wheat breeding programs. However, this is always difficult because of the large number of genes involved and the low heritability estimates (Kronstad and Moss, 1990). Grafius (1964) described grain yield as a complex trait in a geometric form, which consists of three components: the number of spikes per unit area (x), the number of kernels per spike (y), and the average kernel weight (z). Thus, the grain yield per unit area is the product of the three components (x)(y)(z). He proposed that yield might be improved by increasing the weakest component. However, Adams (1967) reported that yield components are interdependent in their development and hence can compensate for each other. Blum (1973) showed that when the number of panicles of sorghum was reduced by drought stress, grain yield of the remaining panicles could be increased either by an increase in number of grains per panicle or production of large grain. Similar compensation in grain size occurs in wheat; however, the potential for compensation by increased grain size or weight is limited (Fischer, 1973). Ginkel et al. (1998) reported that when drought stress occurs during the grain filling period, higher grain yield is associated with high grain number per unit area, low kernel weight and low test weight. Wheat grain yield can also be attributed to change in biological yield, HI or both (Slafer et al., 1994). The total above-ground biomass has not substantially changed over a long period (Austin et al., 1980; Siddique et al., 1989), therefore this trait was not responsible for genetic improvement of grain yield in wheat. Hucl and Baker (1989) reported a positive correlation between grain yield and biomass production in spring wheats. However, harvest index is well correlated with yield increases (Siddique et al., 1989). There is lack of data on the use of harvest index as a selection criterion under dry environments. However, Syme (1972) reported a significant correlation between HI of single plants and mean yield, which provides encouragement for further studies.

2. *Morphophysiological traits*

Over the years several physiological and morphological traits have been suggested for selection to improve grain yield under drought conditions. However, the use of such traits in a breeding program is limited. A number of factors have contributed to this, particularly a) lack of knowledge of the inheritance of these traits, b) insufficient information on the contribution of these traits to higher grain yield over the range of environments encountered in the target area, and c) inability to screen these traits accurately and rapidly in large breeding populations (Blum, 1988). It is mainly for these reasons that plant breeders still rely on the empirical approach, that is, using yield as a selection criterion for drought resistance improvement. However, recently a new level of cooperation has arisen between physiologists and plant breeders to develop the most appropriate plant for particular environment. Richards (1982) termed this breeding approach as analytical, where attributes related to drought resistance are used as selection criteria.

In wheat, grain yield was positively associated with plant dry weight

(Fischer and Wood, 1979) and leaf water contents (Dedio, 1975). Morgan et al. (1986) showed that genotypes with a high capacity for osmotic adjustment have significantly higher yield under field conditions and that the ability of osmoregulation had no effect on yield of these genotypes under favorable conditions. There is no consistent relationship between leaf water potential and grain yield. Kaul (1969) found no correlation between genotype differences in water potential and grain yield, however, Sojka et al. (1981) showed association between leaf Ψ and grain yield, which was specific for particular cultivars. Blum, (1982) observed correlation between leaf Ψ and grain per spike, this however, does not establish association with grain yield, as there may be compensations due to variation in spike number and seed size. Winter et al. (1988) found that higher grain yield was correlated with low leaf water potential because low water potential was associated with maintenance of green leaf tissues. Osmotic potential, which is an essential component of Ψ, was associated positively with grain yield (Keim and Kronstad, 1981). Schonfeld et al. (1988) studied water relation and grain yield of field grown TAM W-101 and Sturdy plants and reported that cultivar TAM W-101 maintained significantly higher RWC than cultivar Sturdy under water stress and had a higher grain yield. They concluded that higher yield in TAM W-101 was attributed to the ability of maintaining higher RWC during water stress. More recently, Steven et al. (1990) also suggested that high RWC and photosynthetic capacity are the traits that may contribute to higher yield and thus drought resistance in cultivar TAM W-101.

Grain yield under water stress also showed positive association with other morphological and physiological traits including: canopy temperature (Blum et al., 1982), colieoptile length (Morgan, 1989), excised leaf water retention (Clark and McCaig, 1982), root system size (Richard and Passioura, 1981), glaucousness (Johnson et al., 1983), early vigor (Turner and Nicholas, 1987), and carbon isotope discrimination (Condon et al., 1990).

Genetic variability and heritability

Sufficient genetic variability must be present for any trait before it can be exploited in a breeding program. Genetic variability in drought resistance exists in crop plants for several attributes (Blum, 1988). Gummuluru et al. (1989) found genotypic variability for various physiological traits in wheat under water stress conditions. Stomatal resistance, CO_2 exchange rate, water-use efficiency, chlorophyll content, leaf area, and shoot dry weight showed high genetic variability. Winter et al. (1988) observed genotypic variability in leaf water potential, seedling survival after desiccation, and excised leaf water retention in winter wheat. They concluded that seedling survival after desiccation was the most suitable technique to screen large breeding populations. Biomass and harvest index were also considered as potential criteria for improving grain yield under drought prone environment (Siddique et al., 1989).

In addition to the above mentioned traits, extensive genetic variability was measured in several morphological and physiological traits to explore them for selecting drought tolerant wheat lines. Sufficient genetic variability was reported for photosynthesis (Austin et al., 1982), canopy temperature (Blum et al., 1982), canopy-air temperature difference (Reynolds et al., 1993), RWC (Schonfeld et al., 1988), osmoregulation (Morgan, 1983), and mobilization of assimilates (Blum, 1983a,b).

Heritability is the function of the observed variance caused by differences in heredity. Heritability expresses the proportion of total variance that is attributable to the average effects of genes in a metric character. The most important function of heritability is its predictive role, expressing the reliability of the observed value as a guide to the breeding value (Falconer, 1989). It is a property, not only of the character, but also of the population and the environmental circumstances to which the individuals are subjected. Plant breeders are interested in heritability to choose an efficient breeding method for a particular trait and to determine the amount of testing necessary to select superior derived lines or individuals (Fehr, 1987). The characters with high heritability values can be improved more rapidly with less intensive evaluation than those with low heritabilities.

Heritability in the broad sense considers total genetic variability in relation to the phenotypic variability, while heritability in the narrow sense considers only the additive portion of genetic variability (Hanson, 1963). Narrow sense heritability is of paramount importance in traditional breeding programs, as plant traits like yield and tolerance to abiotic stresses are controlled by large number of genes, most of which have small effects. When narrow sense heritability is high, mass selection is more reliable, and when it is low, more emphasis must be given to progeny, sib, or family selection (Nyquist, 1991). Knowledge of heritability is also important in deciding early verses late generation of selection. Effective selection in early generations can be achieved only when additive genetic effects are substantial and heritability is high. McKinney et al. (1989) found that selection for a quantitative trait such as canopy temperature depression was not successful in soybean because of low heritability; however, selection for that trait was more successful in advanced $F_{3:4}$ generation.

Genetic studies of drought tolerance in plants are not abundant. A few studies carried out on this aspect have shown encouraging results. Schonfeld et al. (1988) while studying the inheritance of RWC in winter wheat reported that the narrow-sense heritability of RWC increases as drought stress intensified, and reaches a maximum value of 0.64 one weak prior to flag leaf senescence. They also reported that the additive gene effects was more important than dominance effects in the inheritance of RWC.

CHAPTER II

COMPARISION OF METHODS TO QUANTIFY DROUGHT TOLERANCE

Introduction

Limited moisture availability due to low precipitation is a major constraint in winter wheat (*Triticum aestivum* L.) production throughout the Central Great Plains of the USA (Gusta and Chen, 1987). Low moisture at flowering or during grain filling is a characteristic of the environment of this region and other parts of the world where wheat is grown. Drought stress, often accompanied by high temperatures, during the grain filling period affects availability and translocation of photosynthates to the developing grain, resulting in lower kernel weight and grain quality (Hawker and Jenner, 1993).

Stems of wheat and other cereal grains accumulate nonstructural carbohydrates (NSCs) until anthesis; they largely disappear by maturity (McCaig and Clark, 1982). Late season drought markedly reduced the leaf photosynthesis, and then grain growth primarily depended on the remobilization of the stored reserves from the stem (Austin et al., 1980; Wardlaw, 1967). Under favorable postanthesis conditions, the contributions of these carbohydrates to grain filling is relatively low; however, the remobilization and utilization of the stored carbohydrates may be enhanced in response to less favorable conditions for photosynthesis (Haley and Quick, 1993). Pheloung and Siddique (1991) also found greater pre-anthesis NSC contribution to grain filling in drought stressed compared to a well-watered wheat crop.

Blum et al. (1983a,b) proposed the use of a chemical desiccant ($MgClO_4$ applied to the canopy 14 days postanthesis) as a screen for genetic materials that can support grain growth from stored stem NSCs in the absence of photosynthesis. They reported that most of the losses in stem dry weight following desiccation were associated with compensatory increases in kernel growth rate and reductions in kernel weight injury in response to the desiccant. In another study, kernel weight injury by chemical desiccant was positively associated with drought stress injury (Blum et al., 1983b). Few other studies (Haley and Quick, 1993; Nicholas and Turner, 1992; Hossain et al., 1990) also indicated that chemical desiccation may be useful in screening superior genotypes that are tolerant to post anthesis drought stress.

Several other techniques have been developed to screen for drought resistance, e.g., excised leaf water retention (Clark and McCaig, 1982), epicuticular waxes (Johnson et al., 1983), stomatal conductance (Jones, 1977), osmotic adjustment (Morgan, 1983), leaf water potential (Scholander et al., 1965), relative water content (Barrs, 1968), and more recently, canopy temperature depression (Blum et al.,1982) and stay green trait (Rosenow et al., 1988) have been used to evaluate drought tolerance in cereals.

Leaf Ψ and its components are generally considered as reliable measure of the water status of plant tissue. Leaf RWC was later proposed as a better indicator of water status than Ψ (Sinclair and Ludlow, 1985). Canopy temperature and canopy minus air temperature were also found to be reliable indicators of plant water status which in turn is a determinant of grain yield (Jackson et al., 1981). Ehrler et al. (1978) demonstrated that the differences between canopy temperature and air temperature correspond to changes in plant Ψ in wheat under drought stress.

Water stress results in premature plant senescence and shortens the period of photosynthetic activity. Genetic variation for leaf photosynthesis among genotypes was associated with a loss of chlorophyll due to premature leaf senescence (Harding et al., 1990). The SPAD-502 meter has recently been used to quantify leaf greenness in terms of chlorophyll concentration (Ma et al., 1995; Harding et al., 1990). Since leaf photosynthesis is correlated with chlorophyll content, the meter offers a convenient means to assess genotypic variation in photosynthetic rate under drought stress.

All these were attempts to determine suitable selection criteria for drought tolerance in wheat. However, success in breeding to improve drought resistance has been limited by lack of appropriate strategies and screening techniques and lack of knowledge of what determined stress resistance in crop plants. Future yield improvements may be hastened by a better understanding of factors that control growth, development, and yield of cereal (Shorter et al., 1991).

The objectives of this study were to (i) evaluate different techniques for screening winter wheat cultivars for drought tolerance, (ii) study the association between chemical desiccation stress and drought stress, and (iii) determine the potential of chemical desiccation in the greenhouse as a selection tool for postanthesis drought tolerance in the field.

Materials and Methods

Field study

Field experiments were conducted at the Colorado State University, Agricultural Research, Development and Education Center (ARDEC) on Nunn clay loam (fine, montmorillonitic, mesic Aridic Argiustolls) near Fort Collins, CO, and at the Central Great Plains Research Station on Rago silt loam (fine, montmorillonitic, mesic Pachic Argiustolls) near Akron, CO, during the 1995-96 (1996) and 1996-97 (1997) growing seasons. Nine cultivars of winter wheat varying in yield potential, water stress tolerance, plant height, and maturity (Table A1) were evaluated under irrigated and dryland conditions at Fort Collins and only under dryland conditions at Akron to assess the usefulness of chemical desiccation and some other physiological traits as selection tools under dryland conditions.

Irrigated experiments were planted in September 1995 and 1996 at Fort Collins. Field plots consisted of four rows, 4.6 m long and 0.3 m apart during 1996 and 1997 growing seasons. Seed rate was 50 kg /ha. The experiments were arranged in a split plot design with four replications, with nontreated (control) and chemical desiccant (DES) treatments as main plots and cultivars as subplots. The number of days from January 1 to anthesis was recorded when about 50% of spikes in a plot showed exserted anthers in the central one-third of the spike. The chemical desiccant sodium chlorate ($NaClO_3$, 2%W/V @ 125 mL/m) was applied to treated plots ten days postanthesis with a CO_2-propelled backpack spray apparatus.

Dryland experiments were conducted at Akron and Fort Collins to study the association between chemical desiccation stress and environmental stress. All conditions were similar to the irrigated experiments except that seeding rate was reduced to 42 kg/ha and plots were in a randomized complete block design with three replications.

Data on water potential (Ψ) and relative water content (RWC) were taken at anthesis only from dryland plots at Akron in 1996. While leaf chlorophyll contents (CHL) and canopy temperature depression (CTD) data were taken at anthesis and 21 DAA (days after anthesis) from the 1996 experiment at both locations. The anthesis start on June 1st at Akron (Day of year 152) and June 5th (Day of year 156) at Fort Collins. Flowering in early genotypes was about 1 week earlier than the late genotypes. Leaf water potential was measured using the pressure chamber technique (Turner, 1987) on three fully expanded flag leaves of the same age for each cultivar per replication. Relative water content was also determined on three fully expanded flag leaves by using the formula given by Barrs (1968). Immediately after cutting, leaves were sealed inside a plastic bag and placed in a cooler. Fresh weight was determined within 1 h after excision. Turgid weight was obtained after soaking the leaves in distilled water for 16 to 18 h. After soaking, leaves were carefully blotted dry with tissue paper prior to determination of turgid weight. Dry weight was obtained after oven drying the leaves for about 72 h at 65 - 70 °C.

Leaf chlorophyll contents (CHL) were measured on six flag leaves per plot with a self-calibrating chlorophyll meter (Minolta model SPAD 502). CTD measurements were made using a hand-held Infrared Thermometer (IRT) with a field view angle of 2.5 degrees. Two measurements per plot were taken at 1 m from the edge of the plot and approximately 50 cm above the canopy with an angle of 30 degrees from the horizontal (Reynolds et al., 1993). All these measurements were done between 1230 and 1500 h.

Dry matter yield, grain yield (GY), and harvest index (HI) were determined from a harvested area of 1 m from each plot at maturity from irrigated and dryland experiments during 1996 and 1997. The samples were air-dried and weighed to determine the dry matter yield, and then number of spikes (SN) were counted. Number of grains per spike (KS) and kernel weight (KW) were determined on ten randomly selected spikes from each plot. Kernel number (KN) was derived from GY and KW estimates. Test weight (TW; grain volume weight) was estimated from a small sample (approx. 250 g) of the harvested grain.

Greenhouse study

Two sets of greenhouse (GH) experiments were conducted during January-April, 1996. The same cultivars as in the field experiments were grown in pots under well-watered, drought, and chemical desiccant treatments in 1996. The germinated seeds were vernalized at about 2 °C for eight weeks.

Planting was stratified so that all the cultivars flowered at about the same time. The seedlings were transplanted into plastic pots of 6.5 L capacity (23.1 cm x 22.5 cm). Five seedlings were planted per pot and thinned to three. Soil medium was made out of five parts soil (silt loam): one part peat moss. Each pot was brought to field capacity by adding a predetermined amount of water prior to transplanting a seedling into it. The water treatment was calculated based on the water retention curve (capillary pressure saturation curve) as determined by the Soil Testing Laboratory at Colorado State University.

In the well watered (control) treatment, pots were maintained at 100% available soil water until physiological maturity. In the drought stress (WS) treatment, water was withheld at late heading and pots were maintained at 10% available water. In the desiccant (DES) treatment, sodium chlorate (2%W/V @ 125 mL/m) was applied ten days postanthesis and pots were maintained at 100% available water. Each pot was weighed daily and water requirement determined for that particular treatment.

Leaf Ψ and RWC were measured at anthesis on three fully expanded flag leaves using the same procedure as in the field experiments. The experimental design was a randomized complete block design with four replications. Each experimental unit consisted of a pot containing three seedlings. Yield and yield component measurements were taken from each pot.

Data analysis

Statistical analyses were computed using the Statistical Analysis System (SAS; SAS Institute, 1988). Analysis of variance for all measured variables in all experiments (field and greenhouse) was done using the PROC GLM procedure of SAS. Analyses of desiccation injury were conducted, using the following formula for percent injury relative to the control as the response variable in the analysis:

$$\% \text{ injury} = [(\text{Control} - \text{Desiccated}) / \text{Control}] \times 100$$

Analysis of harvest index was conducted using the following formula:

$$\text{Harvest index (HI)} = \text{grain yield} / \text{total shoot biomass yield}$$

Relative water content was calculated from the equation:

$$\text{RWC (\%)} = [(\text{fresh weight} - \text{dry weight}) / (\text{turgid weight} - \text{dry weight})] \times 100$$

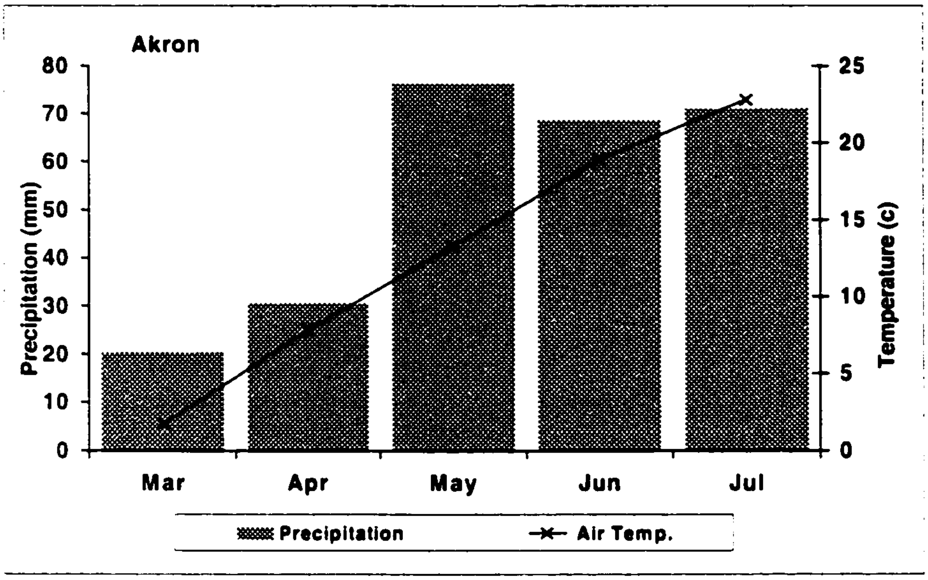
Fisher's Protected Least Significant Difference (LSD) was used to compare means for all measured variables. Simple Pearson correlations between treatment means were calculated using the PROC CORR procedure of SAS.

Results and Discussion

Productivity and yield

Climatological measurements recorded throughout the 1996 and 1997 growing seasons at Fort Collins and Akron, CO. are presented in (Fig.1a and 1b). The mean precipitation of each of the three growing seasons was above average. The mean temperatures were near normal for this region except in 1997 during the month of May and June the mean monthly temperature was below normal.

Mean squares for all measured traits under irrigated and dryland conditions at Fort Collins and Akron are presented in Tables A2 and A3, respectively. At Fort Collins, the Year (YR) x Environment (E) x Cultivar (CV) interaction was significant ($p \leq 0.01$) for harvest index (HI). YR x CV interaction was significant ($p \leq 0.05$) for spike number (SN), test weight (TW), and kernel weight spike^{-1} (SW) at Fort Collins, while significant ($p \leq 0.01$) for TW, HI, and kernel number (KN) at Akron. E x CV interaction at Fort Collins was also significant ($p \leq 0.01$) for grain yield (GY), SW, and HI, and significant ($p \leq 0.05$) for biomass (BIO) and TW. Since significant interactions were found for most of the traits measured (Tables A2 and A3), the analysis of variance was carried out for each year and treatment.



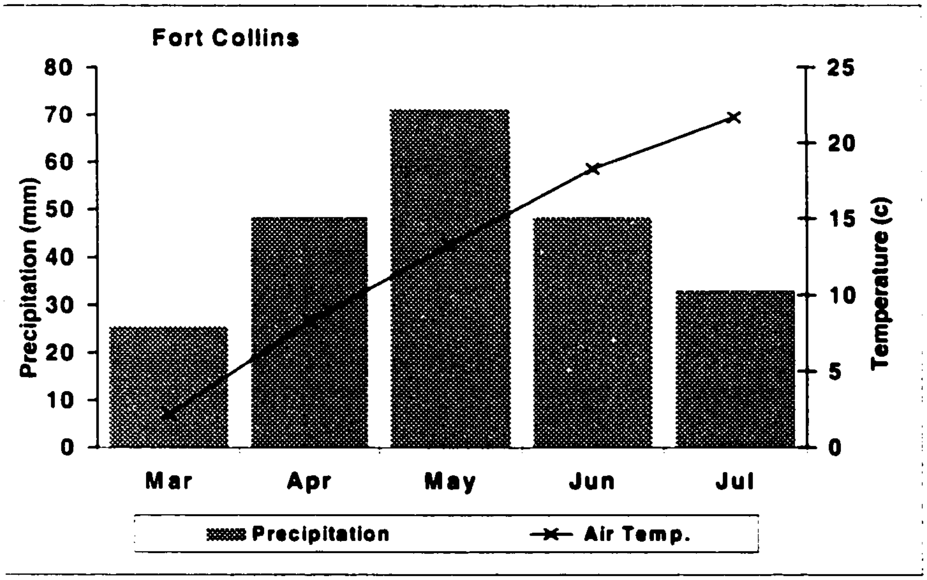


Figure 1a: Long term monthly mean air temperature and precipitation at Akron and Fort Collins over a period of 30 years.

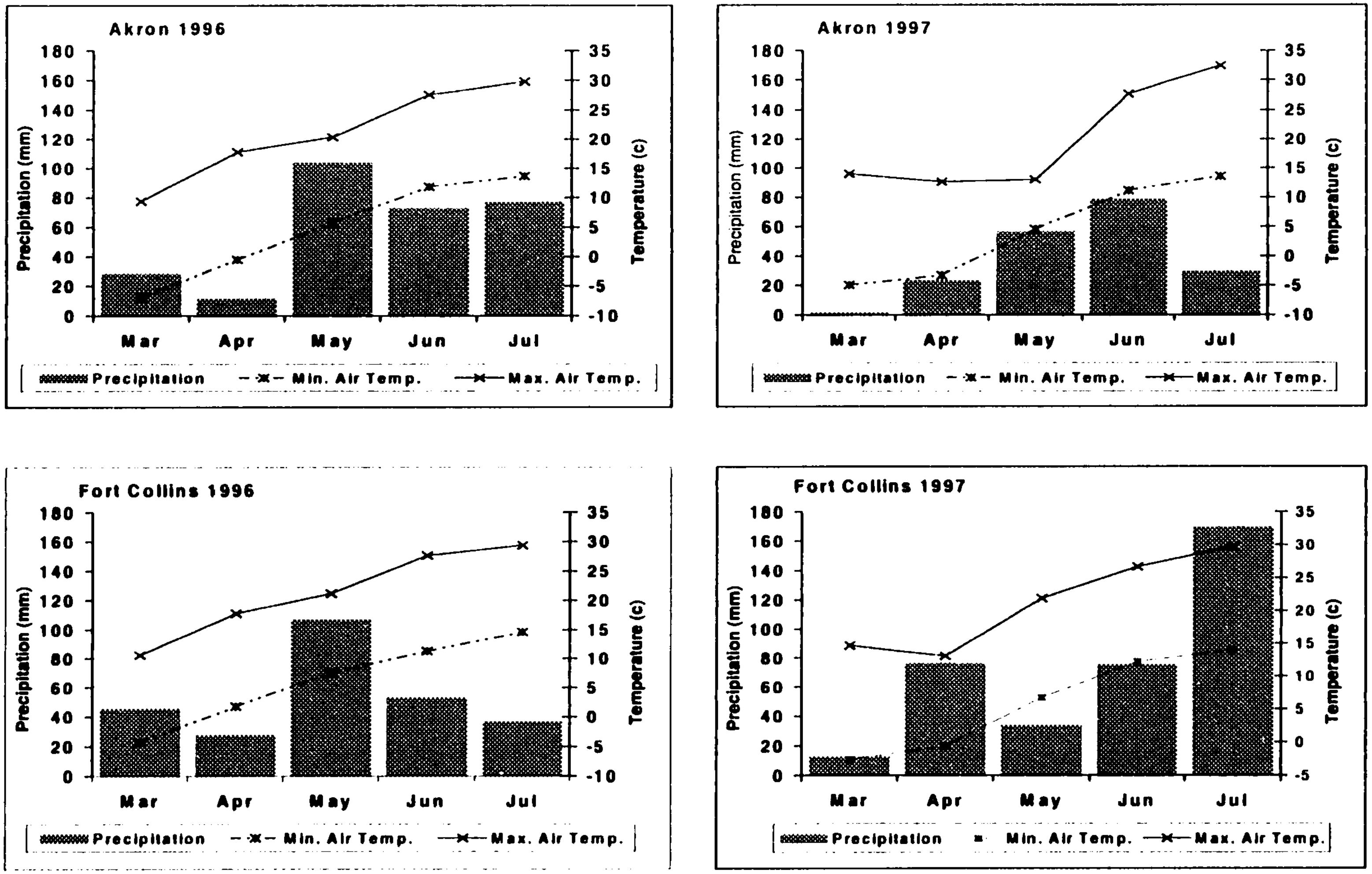


Figure 1b: Monthly mean minimum and maximum air temperature and precipitation at Fort Collins and Akron during the 1996 and 1997 growing season.

Means for traits measured under control and dryland conditions are presented in Table 1 through Table 9, and the correlation coefficients of GY with other variables under six different environments are presented in Table 10. The most consistent genotypic performance in GY and BIO were observed for Sandy (Table 1 and Table 2). In both years the BIO and GY were higher in Sandy (significant only in 1996) than for almost all other cultivars under control plots at Fort Collins. Yuma had the significantly highest GY under dryland conditions at Akron in 1996 and at Fort Collins in 1997 (Table 1). GY and BIO productivity was lower in Sturdy, especially under dryland conditions, presumably due to its drought stress susceptibility (Winter et al., 1988; Morgan et al., 1993). BIO showed strong positive association with GY both under irrigated and dryland conditions (Table 10).

Significant cultivar differences were detected for KW (Table 3) and for KN (Table 4) in both years under control and both dryland (Akron and Fort Collins) conditions. TAM 101 had the highest KW; however, Lamar and TAM 107 also maintained stable KW in both years and almost all environments. Sandy had significantly lower KW across years and environments. In contrast for KN, Sandy had the highest KN and TAM 101 had the lowest KN (Table 4) in both years and environments. TAM 101 also had significantly lower number of kernels spike^{-1} (KS) while Sandy and Lamar had higher KS under control and both dryland locations in both years (Table 6).

GY both in irrigated and dryland conditions was strongly associated with KN in both years, while the association between GY and KW was not significant

(Table 10). The KN, in turn, was associated with KS at four out of six environments and with spike number at only two of the environments (Table 10). The KN correlated more strongly with KS than with SN under dryland conditions. KW was negatively associated with KS and KN at four and two environments, respectively (Table 10). The consistent association of KN with GY supports previous studies with winter wheat which have suggested that KN was more important in determining the wheat yield in the Central Great Plains than other yield components (Morgan et al., 1993; Shanahan et al., 1984 and 1985).

KN was enhanced by irrigation in 1996, but not in 1997 (Table 4). Inability to detect an irrigation effect in 1997 was probably due to the absence of significant water stress for dryland plants during reproductive and grain-filling stages. Under dryland conditions at Fort Collins, KN decreased 0.3% in 1996 and increased 3% in 1997 compared to the control. The SN was also 5% higher in dryland plots in 1997 compared to the control (Table 5). It seems that the increase in KN was mainly due to the increased SN.

TW and SW were enhanced by irrigation in both years (Tables 7 and 8, respectively). The most consistent genotypic variation in TW and SW were observed for Lamar. In both years under control and dryland environments, TW and SW were significantly higher in Lamar than almost all other cultivars. TW in Sturdy was lower both in control and dryland conditions. Sturdy also had lower SW under Akron dryland condition, while under Fort Collins dryland TAM 200 had the lower SW in both years.

Table 1. Mean grain yield (g m^{-2}) for nine cultivars grown under irrigated (control) and dryland conditions in 1996 and 1997.

	1996			1997		
	Fort Collins		Akron	Fort Collins		Akron
Cultivar	Control	Dryland	Dryland	Control	Dryland	Dryland
Agate	603	508	459	530	409	304
Baca	533	398	603	425	401	316
Lamar	612	566	547	517	463	351
Sandy	700	547	566	620	489	338
Sturdy	468	497	435	501	423	230
TAM 101	501	457	449	564	444	278
TAM 107	559	447	552	541	494	326
TAM 200	629	484	528	535	426	383
Yuma	658	587	670	571	573	314
Mean	585	499	534	534	345	315
LSD (0.05)	87	NS	41	NS	70	NS

NS indicates non-significant.

Table 2. Mean biomass (g m^{-2}) for nine cultivars grown under irrigated (control) and dryland conditions in 1996 and 1997.

	1996			1997		
	Fort Collins		Akron	Fort Collins		Akron
Cultivar	Control	Dryland	Dryland	Control	Dryland	Dryland
Agate	1676	1488	1309	1354	1044	824
Baca	1504	1307	1591	1333	1030	843
Lamar	1541	1513	1341	1410	1148	934
Sandy	1749	1480	1376	1441	1172	845
Sturdy	1336	1369	1101	1236	1015	738
TAM 101	1311	1317	1104	1333	1080	788
TAM 107	1351	1246	1351	1234	1038	799
TAM 200	1523	1246	1239	1340	1125	949
Yuma	1521	1487	1586	1404	1273	800
Mean	1501	1384	1333	1343	1103	836
LSD (0.05)	201	299	NS	NS	147	NS

NS indicates non-significant.

Table 3. Mean kernel weight (mg) for nine cultivars grown under irrigation without desiccant (control) and under dryland conditions in 1996 and 1997.

	1996			1997		
	Fort Collins		Akron	Fort Collins		Akron
Cultivar	Control	Dryland	Dryland	Control	Dryland	Dryland
Agate	39.5	36.0	39.9	38.1	33.5	31.4
Baca	33.9	33.9	35.2	34.9	27.9	27.3
Lamar	38.3	36.1	37.4	36.8	27.5	28.9
Sandy	32.9	30.7	32.8	34.4	21.7	23.9
Sturdy	35.7	34.4	34.5	34.6	25.8	22.9
TAM 101	34.8	41.9	40.8	42.0	34.7	31.8
TAM 107	39.4	38.9	36.6	36.5	29.7	31.7
TAM 200	32.8	28.7	31.8	30.7	21.7	24.8
Yuma	36.1	36.2	34.8	35.9	27.7	30.0
Mean	35.9	35.2	36.0	36.0	27.8	28.1
LSD (0.05)	8.0	2.9	2.2	4.1	2.9	2.9

Table 4. Mean kernel number (m^{-2}) for nine cultivars grown under irrigated (control) and dryland conditions in 1996 and 1997.

	1996			1997		
	Fort Collins		Akron	Fort Collins		Akron
Cultivar	Control	Dryland	Dryland	Control	Dryland	Dryland
Agate	15579	14105	8446	13876	12828	7095
Baca	16345	11751	12521	12283	13719	8323
Lamar	13816	15636	10685	14080	14770	9140
Sandy	20637	17783	12567	17939	17889	10490
Sturdy	12006	14416	9234	14473	14523	7310
TAM 101	9273	10958	8031	13415	11790	6395
TAM 107	12260	11488	11043	14911	14578	7478
TAM 200	14869	17067	12144	17467	17807	11283
Yuma	15048	16244	14056	15974	19981	8032
Mean	14426	14383	10970	14936	15321	8394
LSD (0.05)	3360	NS	3445	3409	NS	NS

NS indicates non-significant.

Table 5. Mean spike number (m^{-2}) for nine cultivars grown under irrigated (control) and dryland conditions in 1996 and 1997.

	1996			1997		
	Fort Collins		Akron	Fort Collins		Akron
	Control	Dryland	Dryland	Control	Dryland	Dryland
Agate	655	574	540	649	675	507
Baca	637	539	677	575	632	513
Lamar	532	558	450	510	528	491
Sandy	713	611	584	658	649	508
Sturdy	555	589	487	603	582	495
TAM 101	605	624	474	721	704	515
TAM 107	568	563	536	551	582	478
TAM 200	555	634	606	690	777	642
Yuma	589	611	583	559	680	458
Mean	601	589	549	613	645	512
LSD (0.05)	110	NS	NS	NS	127	NS

NS indicates non-significant.

Table 6. Mean number of kernels $spike^{-1}$ for nine cultivars grown under irrigated (control) and dryland conditions in 1996 and 1997.

	1996			1997		
	Fort Collins		Akron	Fort Collins		Akron
Cultivar	Control	Dryland	Dryland	Control	Dryland	Dryland
Agate	29.8	32.0	31.5	19.9	20.4	24.6
Baca	29.9	31.1	31.9	20.9	22.4	26.5
Lamar	40.6	34.8	36.3	29.8	26.2	29.3
Sandy	38.4	36.4	39.3	31.9	27.7	31.4
Sturdy	31.8	29.9	31.3	25.9	25.8	22.3
TAM 101	24.8	25.8	30.7	18.7	17.4	21.6
TAM 107	32.1	27.2	32.1	25.8	26.4	24.0
TAM 200	38.5	34.7	34.9	27.6	26.0	28.1
Yuma	34.0	35.5	34.6	29.2	30.0	28.0
Mean	33.3	31.9	33.6	25.5	24.7	26.2
LSD (0.05)	5.1	4.5	NS	5.4	3.9	5.2

NS indicates non-significant.

Table 7. Mean test weight (kg m^{-3}) for nine cultivars grown under irrigated (control) and dryland conditions in 1996 and 1997.

	1996			1997		
	Fort Collins		Akron	Fort Collins		Akron
Cultivar	Control	Dryland	Dryland	Control	Dryland	Dryland
Agate	761	753	714	744	713	689
Baca	765	757	718	735	717	697
Lamar	765	770	738	742	722	665
Sandy	776	761	737	717	690	677
Sturdy	740	735	715	703	694	665
TAM 101	761	757	714	740	718	683
TAM 107	761	762	696	711	701	669
TAM 200	759	753	727	703	656	704
Yuma	738	749	708	713	665	680
Mean	758	755	719	723	697	680
LSD (0.05)	24	34	30	34	46	46

Table 8. Mean kernel weight $spike^{-1}$ (g) for nine cultivars grown under irrigated (control) and dryland conditions in 1996 and 1997.

	1996			1997		
	Fort Collins		Akron	Fort Collins		Akron
Cultivar	Control	Dryland	Dryland	Control	Dryland	Dryland
Agate	1.17	1.15	1.26	0.76	0.66	0.77
Baca	1.01	1.05	1.12	0.67	0.66	0.72
Lamar	1.55	1.26	1.36	1.14	0.81	0.83
Sandy	1.27	1.11	1.29	0.98	0.78	0.76
Sturdy	1.13	1.03	1.08	0.90	0.77	0.52
TAM 101	1.11	1.08	1.25	0.77	0.65	0.69
TAM 107	1.25	1.06	1.17	1.03	0.83	0.76
TAM 200	1.26	1.00	1.11	0.82	0.58	0.70
Yuma	1.21	1.29	1.20	1.01	0.70	0.82
Mean	1.22	1.11	1.20	0.90	0.72	0.73
LSD (0.05)	0.14	0.17	NS	0.17	NS	0.15

NS indicates non-significant.

Harvest index (HI) has been defined as the ratio of grain yield to total above ground biomass (Donald and Hamblin, 1976). There has been considerable interest in this trait since almost all increases in cereal yield have been achieved through increases in the HI with little change in biomass yield (Gifford et al., 1984; Turner et al., 1989). In control plots HI averaged 0.39 in 1996 and 0.40 in 1997 (Table 9). In dryland plots at Fort Collins, HI decreased 8% in 1996, and increased 5% in 1997, compared to control plots. At Akron, dryland HI was 10% higher in 1996, while 11% lower in 1997, than Fort Collins dryland plots. The apparent different response of HI was probably due to different seasonal patterns of soil water availability. In 1997 at Fort Collins, precipitation during reproductive and grain filling periods was well above average, and as a result, dryland plots were capable of maintaining HI similar to control plots. Passioura (1977) has suggested that HI is related to the amount of water available after anthesis. Significant cultivar differences were observed for HI in both years of study. In 1996, HI was higher in Yuma, while in 1997, TAM 107 had higher HI in control and both dryland locations.

Chemical desiccation evaluation

Mean squares for traits measured under irrigation without desiccant (control) and with chemical desiccant at Fort Collins are presented in Table A4. Highly significant ($p \leq 0.01$) differences between the two years were observed for BIO and kernels spike^{-1} (KS) and difference between years for HI was also significant ($p \leq 0.05$). Highly significant ($p \leq 0.01$) differences between the desiccant treatments were found for all the traits measured except SN.

Table 9. Mean harvest index for nine cultivars grown under irrigated (control) and dryland conditions in 1996 and 1997.

	1996			1997		
	Fort Collins		Akron	Fort Collins		Akron
Cultivar	Control	Dryland	Dryland	Control	Dryland	Dryland
Agate	0.36	0.34	0.35	0.44	0.39	0.37
Baca	0.36	0.30	0.38	0.36	0.39	0.37
Lamar	0.40	0.37	0.41	0.43	0.40	0.38
Sandy	0.40	0.37	0.41	0.32	0.42	0.40
Sturdy	0.35	0.36	0.40	0.40	0.42	0.31
TAM 101	0.38	0.35	0.41	0.41	0.41	0.36
TAM 107	0.41	0.36	0.41	0.42	0.48	0.41
TAM 200	0.41	0.39	0.43	0.39	0.38	0.40
Yuma	0.43	0.39	0.43	0.41	0.45	0.39
Mean	0.39	0.36	0.40	0.40	0.42	0.38
LSD (0.05)	0.03	0.02	0.03	0.06	0.05	0.04

Table 10. Pearson correlation coefficients among yield and yield components under different environmental conditions in 1996 and 1997.

	1996 environments			1997 environments		
Variables	Fort Collins Control	Fort Collins Dryland	Akron Dryland	Fort Collins Control	Fort Collins Dryland	Akron Dryland
Grain yield vs. Biomass	0.82**	0.80**	0.89**	0.21	0.71*	0.91**
Grain yield vs. Harvest index	0.64*	0.77**	0.39	0.85**	0.73*	0.85**
Grain yield vs. Kernel no.	0.75**	0.76**	0.93**	0.72*	0.69*	0.78**
Grain yield vs. Kernel wt.	-0.44	0.15	-0.44	0.14	0.01	-0.02
Kernel no. vs. Spike no.	0.67*	0.45	0.68*	0.25	0.25	0.62
Kernel no vs. Kernel spike^{-1}	0.54	0.92**	0.59	0.75**	0.87**	0.82**
Kernel wt. vs. Kernel spike^{-1}	-0.63*	-0.73**	-0.57	-0.57	-0.60	-0.35
Kernel no. vs. Kernel wt.	-0.74*	-0.75**	-0.74*	-0.57	-0.64*	-0.61

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

Year x desiccant (YR x DES) interaction effects were highly significant ($p \leq 0.01$) for SN, HI, KW, GY, and TW, but not for KS and BIO. YR X DES interaction was not due to change in treatment ranking between years, but to the differences between the two treatments.

Mean squares for analysis based on desiccation injury are presented in Table A5. Highly significant ($p \leq 0.01$) differences between both years were observed for GY injury, TW injury, KW injury, SW injury, although not for KS injury. Year and cultivar (YR x CV) interaction was highly significant ($p \leq 0.01$) only for TW injury. This interaction was mainly due to change in ranking of the cultivars tolerance to the chemical desiccation.

The means for GY injury and TW injury are presented in Table 11. The GY injury was significant only at $p \leq 0.06$. GY injury from chemical desiccant ranged from 33.1 to 58% in 1996 and 10.2 to 52.2% in 1997. Sandy and TAM 200 suffered the higher injuries and Lamar, TAM 101, and TAM 107 showed relatively lower GY injury. TW injury ranged from 4.3 to 25.0% in 1996 and from 3.6 to 8.8% in 1997. Lamar suffered significantly lower TW injury and Sandy suffered significantly higher TW injury over the two years.

The KW injury ranged from 24.2 to 50.3% in 1996 and 12.1 to 36.8% in 1997 (Table 12). The injury to SW ranged from 27.2 to 54.5% in1996 and 5.4 to 43.5% in 1997 (Table 13). Sandy and TAM 200 exhibited significantly higher injury for both KW and SW over the two years. TAM 101 and TAM 107 showed significantly lower injury for KW. KN and KS was insensitive to the chemical desiccation treatment (Table 12 and 13, respectively). The cultivars were not

Table 11. Means for grain yield and test weight injuries at Fort Collins in 1996 and 1997.

Cultivar	Grain yield injury†			Test weight injury		
	1996	1997	Mean	1996	1997	Mean
	%					
Agate	41.2	10.2	25.7	7.2	3.6	5.4
Baca	41.2	26.2	33.7	10.3	6.8	8.6
Lamar	35.3	34.3	34.8	4.8	5.8	5.3
Sandy	57.6	52.2	54.9	25.0	8.3	16.7
Sturdy	40.3	40.4	40.4	7.0	5.2	6.1
TAM 101	33.1	30.7	31.9	7.4	5.0	6.2
TAM 107	34.4	32.5	33.5	7.5	5.1	6.3
TAM 200	58.3	30.4	44.4	7.9	8.8	8.4
Yuma	50.6	38.2	44.4	7.9	5.7	6.8
Mean	43.6	32.8	38.2	9.4	6.0	7.7
LSD (0.05)						
Cultivar	17.6			3.4		
Year	8.3			1.7		

† Calculated as % injury = (Control-desiccated) / Control x 100 for each desiccation injury variable.

significantly different for KN injury and KS injury over the two years; however, some cultivars showed increased KN (Lamar in 1996) and KS (Agate, Baca, and TAM 101 in 1997) to chemical desiccation treatment. Haley and Quick (1993) reported that lower concentration of potassium iodide (0.15%) induces increases in KN compared to the control treatment. In our study, the rainy conditions during the first part of the June 1997 may have reduced the efficacy of chemical desiccation, at least for some cultivars, thus inducing an increase in KS in 1997.

The reduction in biomass among cultivars due to chemical desiccation was not significant, while reduction in HI ranged from 20.5 to 46.6% in 1996 and 2.3 to 34.7% in 1997 (Table 14). As for other traits, Sandy (40.7%) and TAM 200 (30.3%) showed significantly higher injury for HI over the two years.

Chemical desiccation injury was greater in 1996 than in 1997 for almost all the traits measured. The reason for significantly lower injury in 1997 was the mild and rainy weather during the critical period of chemical desiccant application. The concept of the chemical desiccation method is based on the complete elimination of the photosynthetic source, and thus the developing grain growth depends on the stem soluble carbohydrate storage and its mobilization (Blum et al., 1983a). In our study, rainy weather may have resulted in incomplete senescence of photosynthetic tissues of the plant; thus causing lower or no injury for some cultivars, particularly the late maturing cultivar Agate.

Sandy and TAM 101 were the most sensitive to chemical desiccant, while Lamar and TAM 101 were tolerant to chemical desiccation. Agate, Baca, and TAM 107 showed moderate tolerance to chemical desiccation. Sandy has been reported by some workers (Morgan et al., 1993, Martin et al., 1993 , Morgan and LeCain, 1991) to maintain adequate yield under drought conditions. In our study under chemical desiccation stress, Sandy was least tolerant; however, under dryland conditions both at Akron and Fort Collins, Sandy's yield was above the location mean grain yield in both years. This may be simply due to the high yield potential of Sandy or there might be some other drought tolerance mechanisms operating in this cultivar that confer tolerance to environmental drought stress. Drought tolerance not only depends on the contribution of stem reserves, but also on some other characters, such as osmotic adjustment and continued water uptake through deep rooting (Morgan and Condon, 1986; Turner, 1986). Lamar and TAM 107 performed better under desiccation stress as indicated from their lower GY injury and TW injury. TAM 101 has been reported from various workers (Hossain et al.,1990, Fjell et al., 1985) to have stable KW, and also in our study, TAM 101 had significantly higher KW across environments in both years, and thus showed greater tolerance to desiccation injury, as indicated from its lower GY and KW injuries. Hossain et al. (1990) also reported that cultivars with higher kernel weight suffered lower desiccation injury which is in agreement with this study. Blum et al. (1983b) reported that partial removal of kernels from the spike increased the weight of remaining kernels under chemical desiccation. TAM 101 also had lower KS in both years, which may be one reason why it maintained higher kernel weight and had greater tolerance to chemical desiccation.

Table 12. Means for kernel weight and kernel number injuries at Fort Collins in 1996 and 1997.

Cultivar	Kernel weight injury†			Kernel number injury		
	1996	1997	Mean	1996	1997	Mean
	%					
Agate	28.6	12.1	20.4	10.5	4.1	7.3
Baca	33.5	19.8	26.7	9.9	6.9	8.4
Lamar	40.8	25.1	33.0	-14.2	12.5	-0.9
Sandy	45.4	36.8	41.1	23.6	23.1	23.4
Sturdy	30.5	25.4	28.0	14.8	20.1	17.5
TAM 101	31.0	17.3	24.2	2.1	15.9	9.0
TAM 107	24.2	15.8	20.0	6.0	20.6	13.3
TAM 200	50.3	29.0	39.7	18.5	1.8	10.2
Yuma	36.9	22.9	29.9	19.2	18.2	18.7
Mean	35.7	22.7	29.2	10.0	13.7	11.9
LSD (0.05)						
Cultivar	11.1			NS		
Year	5.3			NS		

NS indicates non-significant.

† Calculated as % injury = (Control-desiccated) / Control x 100 for each desiccation injury variable.

Table 13. Means for spike weight and kernel spike^{-1} injuries at Fort Collins in 1996 and 1997.

Cultivar	Spike weight injury† 1996	Spike weight injury† 1997	Spike weight injury† Mean	Kernel spike^{-1} injury 1996	Kernel spike^{-1} injury 1997	Kernel spike^{-1} injury Mean
	------------------------------	---	%	---	------------------------------	
Agate	37.2	8.4	22.8	13.7	-8.4	2.7
Baca	35.1	5.4	20.3	3.6	-10.8	-3.6
Lamar	51.6	40.9	46.2	19.9	13.3	16.6
Sandy	54.5	43.5	49.0	19.9	22.4	21.2
Sturdy	42.1	31.7	36.9	16.6	6.9	11.8
TAM 101	34.0	9.2	21.6	4.7	-9.3	-2.3
TAM 107	27.2	34.2	30.7	3.8	5.5	4.7
TAM 200	53.0	33.4	43.2	2.1	5.5	3.8
Yuma	46.0	36.3	41.2	12.1	13.6	12.9
Mean	42.3	27.0	34.7	10.7	4.3	7.5
LSD (0.05)						
Cultivar	11			NS		
Year	5			NS		

NS indicates non-significant.

† Calculated as % injury = (Control-desiccated) / Control x 100 for each desiccation injury variable.

Table 14. Means for biomass and harvest index injuries at Fort Collins in 1996 and 1997.

	Biomass injury†			Harvest index injury		
Cultivar	1996	1997	Mean	1996	1997	Mean
	------------------------------ %			------------------------------		
Agate	18.1	-0.7	8.7	28.8	11.3	20.1
Baca	16.5	23.4	20.0	29.7	2.3	16.0
Lamar	19.6	26.7	23.2	20.5	14.3	17.4
Sandy	22.3	28.4	25.4	46.6	34.7	40.7
Sturdy	24.3	32.0	28.2	22.0	12.5	17.3
TAM 101	15.5	26.3	20.9	20.6	6.1	13.4
TAM 107	16.2	20.3	18.3	22.8	15.9	19.4
TAM 200	23.1	18.4	20.8	45.9	14.7	30.3
Yuma	12.7	32.2	22.5	43.3	8.0	25.7
Mean	18.7	23.0	20.9	31.1	13.3	22.2
LSD (0.05)						
Cultivar	NS			15.6		
Year	16.7			7.5		

NS indicates non-significant.

† Calculated as % injury = (Control-desiccated) / Control x 100 for each desiccation injury variable.

Pearson correlations were calculated between the variables measured in the experiments and desiccation injury variables in both years of study (Table 15). Test weight was not associated with any desiccation injury variables in both years, while KW showed highly significant positive association ($r=-0.78^{**}$) with GY injury in 1996, and with TW injury ($r=-0.73^{**}$) in 1997. Both GY and KN were highly significantly associated with GY injuries ($r=0.70^{**}$ and 0.89^{**}, respectively) only in 1996. KN also showed a significant association with KW injury in both years ($r=0.78^{**}$ and 0.73^{*}). Neither GY nor KN was associated with KN injury in both years.

Associations with GY injury were calculated to assess the importance of the other variables in determining the GY injury, and revealed highly significant association with KW injury in both 1996 and 1997 years ($r=0.78^{**}$ and 0.83^{**}, respectively). TW injury was highly significantly associated with KW injury only in 1997 ($r=0.82^{**}$), while TW injury was not significantly associated with GY injury in both years. KN injury showed a highly significant ($r=0.81^{**}$) association with GY injury in 1996 and significant ($r=0.69^{*}$) association in 1997. The association of GY injury was stronger with KW injury ($r=0.85^{**}$) than with KN injury ($r=0.53^{**}$) over the two years.

Chemical desiccation and drought stress

Highly significant ($p\leq0.01$) differences were observed between the treatments for BIO, GY, KW, TW, SW, KS, and KN in both years (Table A6). Highly significant ($p\leq0.01$) year x desiccant (YR x DES) interaction was observed for HI, KW, and TW. The YR x DES interaction for BIO and SW was also

Table 15. Pearson correlation coefficients between variables measured at Fort Collins in 1996 and 1997.

	Grain yield injury†	Test weight injury	Kernel weight injury	Kernel no. injury	Control grain yield	Control kernel weight	Control test weight
1996							
Test weight injury	0.59						
Kernel weight injury	0.78**	0.40					
Kernel no. injury	0.81**	0.53	0.32				
Control grain yield	0.70*	0.52	0.64	0.40			
Control kernel weight	-0.78**	-0.47	-0.63	-0.64*	-0.44		
Control test weight	0.04	0.53	0.25	-0.23	0.31	-0.03	
Control kernel no.	0.89**	0.63	0.78**	0.61	0.90**	-0.78**	0.26
1997							
Test weight injury	0.51						
Kernel weight injury	0.83**	0.82**					
Kernel no. injury	0.69*	-0.13	0.26**				
Control grain yield	0.53	0.14	0.39	0.32			
Control kernel weight	-0.28	-0.73*	0.61	0.27	0.13		
Control test weight	-0.53	-0.45	-0.48	-0.07	-0.22	0.63	
Control kernel no.	0.61	0.64	0.73*	0.03	0.73*	-0.57	0.64*

*, ** Significant at the 0.05 and 0.01 probability levels, respectively (n=9).

† Calculated as % injury = (Control-desiccated) / Control x 100 for each desiccation injury variable.

significant ($p \leq 0.05$). The year x cultivar (YR x CV) interaction was also highly significant ($p \leq 0.01$) for HI and TW, and significant ($p \leq 0.05$) for SW and KS. This YR x CV interaction was due to the change in ranking of the cultivars between the two years, particularly, for the drought stress treatment. The injury caused by chemical desiccant and by drought stress was significantly different for all the traits except KS (Table A7). The mean reduction in GY, KW, TW, and in KN caused by chemical desiccant was significantly higher than caused by drought stress in both years 1996 and 1997 (Fig. 2).

Yield obtained after chemical desiccation was not significantly associated with dryland yield at both locations in both years (Table 16 and 17). Desiccated KW was strongly and positively associated with dryland KW at both locations in both years; however, the association was stronger in 1996 at both Akron and Fort Collins ($r=0.88^{**}$ and 0.92^{**}, respectively). The association between desiccated yield and dryland KW was positive but significant only in 1996 at both Akron and Fort Collins ($r=0.78^{**}$ and 0.65^{*}, respectively). Hossain et al. (1990) also reported a positive association between desiccated yield and dryland KW. KN under dryland was negatively associated with desiccated KW, at both locations in both years. GY injury and KW injury was strongly and negatively associated with dryland KW. The correlation between chemical desiccant and drought induced reduction in GY and yield component was not significant for almost all the traits studied. The association between the reduction in KW due to chemical desiccation and to drought stress was weak but positive both in 1996 and 1997 ($r=0.55$ and 0.57; $n=9$, respectively). A stronger association may be

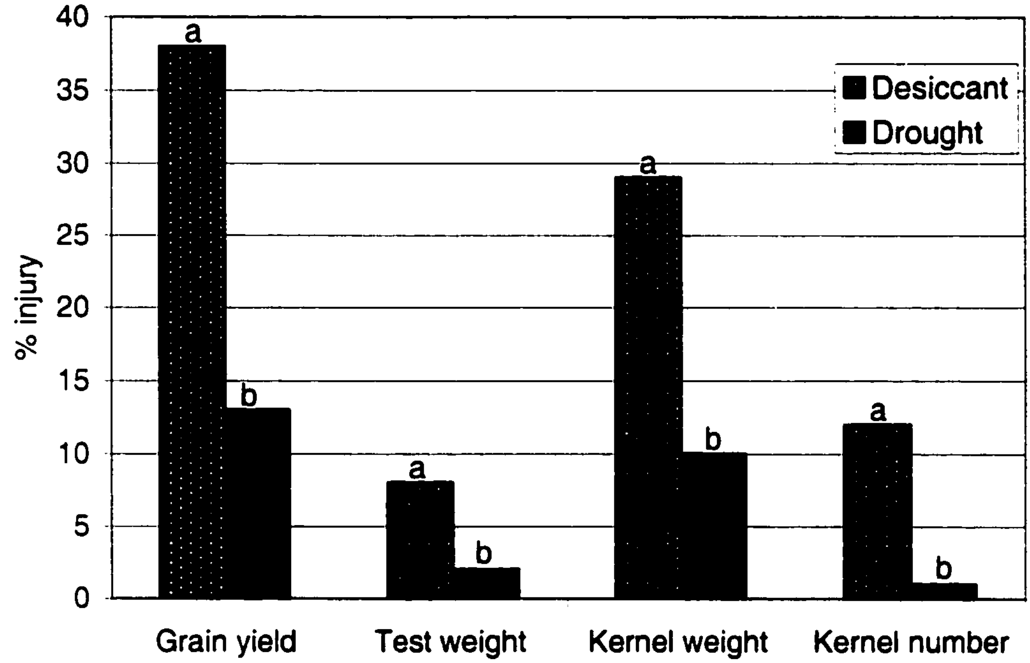


Figure 2. Mean percent injury for grain yield, kernel weight, test weight, and kernel number due to chemical desiccant and to drought stress at Fort Collins over 1996 and 1997.

expected, when KW is the main yield component affected by both the chemical desiccant and drought treatments, but was not the case in this study. For both years, the GY under control and dryland conditions was strongly associated with KN (0.88** and 0.70**, respectively), while under chemical desiccant treatment, a stronger association of GY was observed with KW (0.63**) than with KN (0.10). This suggests that under strong stress condition KW become more important yield component.

Blum et al. (1983b) reported that reduction in KW caused by drought and chemical desiccant was positively associated with non-stress KW. However, in our study, we found that reduction in KW by chemical desiccant and by drought was negatively associated with non-stress KW. Thus the selection for small kernel size in environments prone to a single postanthesis drought may not be appropriate as proposed by Blum et al. (1983b). Nicolas and Turner (1992) did not find any correlation between non-stress KW and KW reduction due to drought or desiccant. This suggests that these relationships are either material- or chemical desiccant- specific. A major difference among these studies was the chemical desiccant used which may have different effects on grain growth. Blum et al. (1983a,b) used magnesium chlorate, Nicolas and Turner (1992) used potassium iodide, and we used sodium chlorate.

The ranking of varieties by the chemical desiccant treatment was consistent between years as indicated by the comparison of the KW injury in 1996 and 1997 (Fig. 3). The relationship between KW injuries for the two years was non-linear, and the differences in this relationship between the two years

Table 16. Pearson correlation coefficients between variables measured under irrigation treated with chemical desiccant at Fort Collins and under dryland conditions at Akron in 1996 and 1997.

		Dryland			
Variables	Year	Grain yield	Kernel weight	Test weight	Kernel number
Desiccant yield	1996	-0.08	0.78**	-0.17	-0.38
	1997	0.02	0.60	0.43	-0.25
Yield injury[†]	1996	0.38	-0.79**	0.41	0.64
	1997	-0.01	-0.57	-0.47	0.40
Desiccant kernel wt.	1996	-0.46	0.88**	-0.66*	-0.81**
	1997	-0.44	0.85**	-0.08	-0.72*
Kernel weight injury	1996	0.29	-0.66*	0.79**	0.52
	1997	0.32	-0.81**	-0.06	0.80**
Desiccant test wt.	1996	0.31	0.53	-0.24	-0.38
	1997	0.31	0.71*	-0.15	-0.71*
Test weight injury	1996	0.23	0.66*	0.41	0.37
	1997	0.61	0.81**	0.40	0.90**
Desiccant kernel no.	1996	0.34	-0.38	0.43	0.44
	1997	0.57	-0.35	0.58	0.70*
Kernel no. injury	1996	0.20	-0.62	-0.09	0.42
	1997	-0.40	-0.08	-0.76*	-0.21

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

† Calculated as % injury = (Control-desiccated) / Control x 100 for each desiccation injury variable.

Table 17. Pearson correlation coefficients between variables measured under irrigation treated with chemical desiccant and under dryland conditions at Fort Collins in 1996 and 1997.

Variables	Year	Dryland			
		Grain yield	Kernel weight	Test weight	Kernel number
Desiccant yield	1996	0.11	0.65	0.51	-0.38
	1997	0.11	0.26	-0.04	-0.26
Yield injury[†]	1996	0.35	-0.84**	-0.18	0.82**
	1997	0.51	-0.26	-0.34	0.56
Desiccant kernel wt.	1996	-0.31	0.92**	-0.04	-0.81**
	1997	-0.13	0.87**	0.63	-0.72*
Kernel weight injury	1996	0.40	-0.77**	0.18	0.81**
	1997	0.24	-0.66	-0.48	0.65
Desiccant test wt.	1996	-016	0.38	0.12	-0.39
	1997	-0.23	0.75*	0.81**	-0.71*
Test weight injury	1996	0.14	-0.45	0.15	0.42
	1997	0.03	-0.74*	-0.34	0.59
Desiccant kernel no.	1996	0.50	-0.48	0.51	0.69*
	1997	0.01	-0.75*	-0.79	0.56
Kernel no. injury	1996	0.04	-0.55	-0.56	0.55
	1997	0.60	0.31	0.01	0.76*

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

[†] Calculated as % injury = (Control-desiccated) / Control x 100 for each desiccation injury variable.

may be due to the relatively lower injury by the chemical desiccant in 1997. However, ranking of the cultivars was quite different between the two years in the dryland treatment. Mahalakshmi et al. (1994) also reported that the ranking under drought conditions in the two years was not similar among pearl millet hybrids, which is in accordance with the present study. Mahalakshmi et al. (1994) and Nicolas and Turner (1992) also found that ranking among genotypes under chemical desiccant treatment was consistent between years. These and other studies with a chemical desiccant (Blum et al., 1983a; and Hossain et al., 1990) suggest that desiccant-induced drought stress may be a useful selection technique, particularly under environmental conditions where drought is the major fluctuating constraint during grain filling.

Greenhouse study

Mean squares for all measured traits are presented in Table A8. The treatments were significantly different ($p \leq 0.001$) for BIO, SN, GY, KW, and SW. KS was not affected by the stress treatments. Highly significant variations were observed among cultivars for all the variables measured. Treatment x cultivar interaction was significant only for KW, suggesting that treatments affected the cultivars differently for KW. TAM101 and Agate had significantly higher KW than the other cultivars in the irrigated control and water stress pots, respectively. The GY injury ranged from 14.4 to 60.1% and KW injury ranged from 17 to 53% (Table 18). Agate was the most tolerant to the chemical desiccation, as indicated by its lower GY (14.4%) and KW injuries (18.2%), while TAM 200 showed higher GY (60.1%) and KW injuries (53%) (Table 18). Baca also showed lower GY and

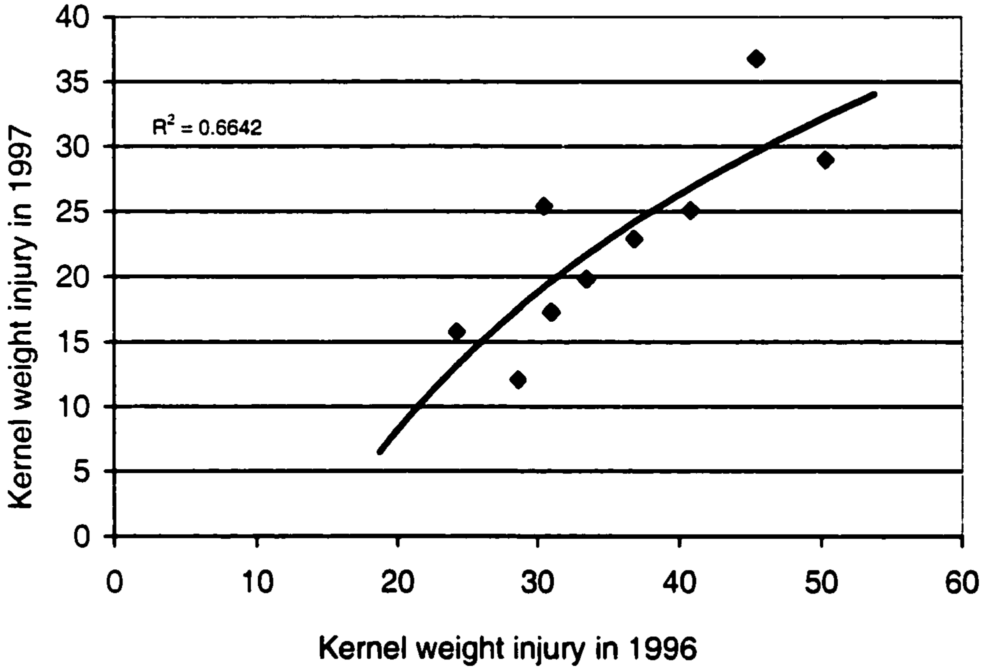


Figure 3. Association between 1996 and 1997 kernel weight injuries due to chemical desiccation.

KW injuries. TAM 200 was also suffered higher chemical desiccation injury in the field trails over the two years. Baca and Sandy showed lower desiccation injury compared to the field.

The injury caused by chemical desiccant and by drought was significantly different for GY and KW (Table 18). The mean GY reduction due to chemical desiccant and to water stress was 44.9 and 8.6%, respectively. Means for BIO, SN, KS, SW are presented in Table A9 and Table A10. The yield component SN in irrigated pots was significantly higher (11.8) than in the water stress treatment; while, KS and SW was not significantly different between the irrigated and water stress treatments. Lamar had the highest GY, BIO, and SW and TAM 200 had the lowest BIO, while TAM 107 had the lowest GY and SW across treatments (Tables A9 and A10).

Within the irrigated treatment, GY was strongly associated with BIO (0.95), SN (0.95), SW (r=0.87), and KS (0.80). KS and KW were negatively associated (r= -0.56). GY was not associated with KW (r= -0.17).

Within the water stress treatment, GY was strongly associated with BIO, SN, SW, and KS (r=0.86,0.80, 0.81, and 0.83, respectively). SW was associated with KS (r=0.84) but not with KW (r=0.04). KW was negatively but not significantly associated with KS (r= -0.50) and GY (r= -0.21).

Under the chemical desiccant treatment, GY was strongly associated with BIO (r=0.96) and SW (r=0.88). GY was positively but not significantly associated with both KW (r=0.43) and KS (r=0.55). In the field study, GY was also weakly associated with KW under irrigated and dryland conditions; however, under the chemical desiccant treatment, KW showed a stronger association with GY than KN. In the GH experiment, KW showed stronger association with GY under desiccant treatment than under water stress and well watered treatments.

The greenhouse (GH) study was conducted to determine the potential of chemical desiccation in the GH as a selection tool for postanthesis drought tolerance in the field. Generally, the magnitude of desiccation injury was the same between the field and GH; however, the ranking of some cultivars changed, particularly Agate, Lamar and TAM 107 for GY injury and TAM 107 for KW injury. The cultivars with larger kernel size generally suffered less desiccation injury in the field, but in the GH, this relationship was not significant. Kernel weight reduction in the field and GH was significantly different; however, the reduction in GY and KS was not significantly different (Fig. 4). There was no significant association between the field and GH for GY injury (r=0.08) and KW injury (r=0.12). Mulat (1998) also utilized chemical desiccation in the GH to screen wheat lines and cultivars for postanthesis stress and reported that 2% sodium chlorate did not cause significant reduction in GY and KW for most of the lines and cultivars. He also observed that the chemical desiccant induced stimulatory responses for kernels spike^{-1}. On the basis of our results, the chemical desiccant may not be useful in the greenhouse to identify the desiccation tolerant genotypes. Further studies are needed to explore the opportunity to utilize chemical desiccants in the greenhouse, particularly for the desiccant concentration and mode of application

Table18. Means for variables measured under well watered (control) and water stress conditions in the greenhouse, 1996.

Cultivar	Control grain yield (g)	% Yield injury†	Control kernel wt. (mg)	% Kernel wt. injury	Stress yield (g)	Stress kernel wt. (mg)
Agate	10.9	14.4	45.0	18.2	9.7	50.7
Baca	10.3	31.3	39.4	17.0	9.0	39.3
Lamar	17.6	53.9	43.8	27.6	10.5	46.5
Sandy	14.7	52.5	40.4	34.8	14.6	39.1
Sturdy	11.2	46.3	36.8	19.3	11.8	43.7
TAM 101	8.1	38.7	47.7	20.2	6.4	47.0
TAM 107	8.1	52.5	45.8	41.4	6.9	43.0
TAM 200	8.6	60.1	38.5	53.5	6.2	40.4
Yuma	12.0	54.6	39.6	40.9	10.8	41.9
Mean	11.3	44.9	41.9	30.4	9.5	43.4
LSD (0.05)	5.5	34	4.4	13.1	5.6	6.4

† Calculated as % injury = (Control-desiccated)/ Control x 100 for each desiccation injury variable.

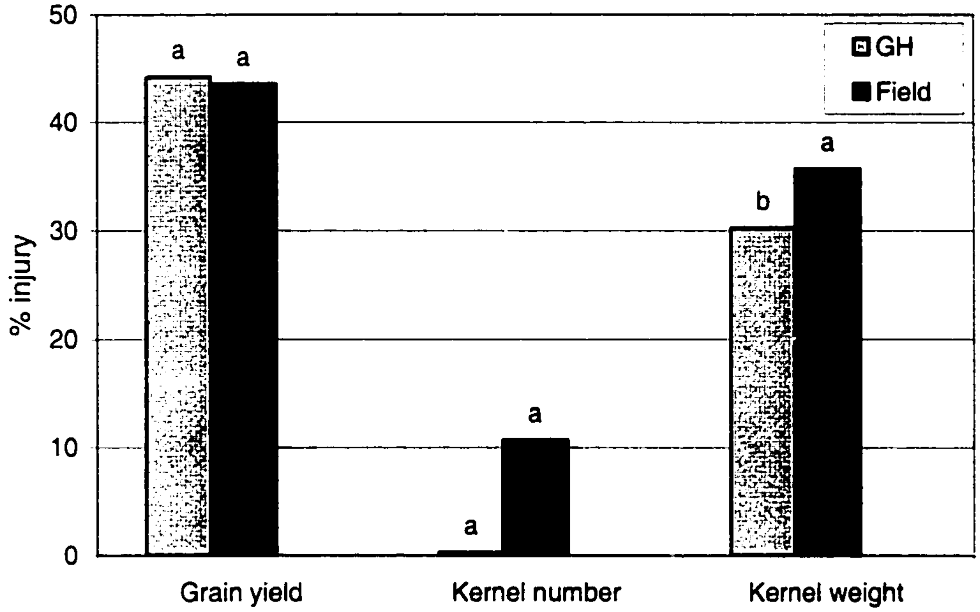


Figure 4. Association between the field and greenhouse (GH) chemical desiccation injury over nine cultivars in 1996.

Physiological study

Analyses of variance showed highly significant ($p \leq 0.01$) differences among cultivars for Ψ and RWC in the GH (Table A11), and at Akron dryland, significant differences were found only for RWC (Table A12). Highly significant differences were observed between the treatments for Ψ and RWC in the GH. Treatment x cultivar interaction was significant only for Ψ (Table A10).

The average leaf Ψ and RWC in the GH was -2.3 Mpa and 82.7% respectively (Table 19). The water stressed pots had -0.33 Mpa lower Ψ and 2.3% lower RWC than the irrigated pots. Yuma had significantly lower leaf Ψ than all the other cultivars, followed by TAM 200. Lamar maintained relatively high Ψ under water stress, while Sturdy had higher Ψ under well watered conditions (Table 19). Leaf RWC of TAM 101 was significantly higher than other cultivars in both irrigated and water stress conditions. Agate and Sturdy showed significantly lower RWC in the GH; however, under Akron dryland conditions, Agate showed significantly higher RWC than all the other cultivars. There was no significant difference in Ψ between Sturdy and TAM 101; however, TAM 101 maintained significantly higher RWC than Sturdy under water stress conditions, which agrees with Schonfeld et al. (1988). Other workers also attributed drought resistance in TAM 101 to its high RWC maintenance, especially under soil water deficit (Johnson et al., 1983; Steven et al., 1990). There was no significant association between Ψ and RWC in the field (0.16) and in the GH (0.43).

Table 19. Mean water potential and relative water content for nine cultivars grown in the greenhouse under irrigated (IR) and water stress (WS) conditions and under field dryland conditions at Akron in 1996.

	Water potential			Relative water content		
	Greenhouse		Field	Greenhouse		Field
Cultivar	IR	WS	dryland	IR	WS	dryland
	----- Mpa -----			----- % -----		
Agate	-2.09	-2.56	-2.13	81.6	78.7	87.4
Baca	-2.13	-2.58	-2.00	82.9	80.5	83.7
Lamar	-2.17	-2.39	-1.92	85.8	81.6	84.3
Sandy	-2.05	-2.43	-2.14	83.4	82.2	80.9
Sturdy	-1.95	-2.47	-2.06	82.7	79.7	80.0
TAM 101	-2.16	-2.49	-2.09	86.2	87.5	81.0
TAM 107	-2.02	-2.43	-2.13	84.7	84.0	81.3
TAM 200	-2.10	-2.75	-2.10	82.7	81.3	80.6
Yuma	-2.08	-3.04	-2.11	82.0	81.5	84.8
Mean	-2.08	-2.57	-2.08	83.6	81.9	82.7
LSD (0.05)						
Treatment	0.08		--	1.35		--
Cultivar	0.17		NS	2.86		4.65
T x CV	0.31		--	NS		--

NS indicates non-significant.

Highly significant differences were observed between the treatments, for canopy temperature depression (CTD) at Fort Collins at both dates of measurement. The cultivars had significant variations for CTD at anthesis and 21 DAA (days after anthesis) at Fort Collins, while at Akron CTD was significant only at 21 DAA (Table A11 and A12). The most consistent genotypic variation in CTD was observed for TAM 107. At both dates of measurement, CTD was significantly lower in TAM 107 (warmer canopy) than all the other cultivars, particularly under drought stress at Fort Collins (Table 20). Agate and Yuma maintained cooler canopies (high CTD) in all the environments at both dates. Baca and Sandy also had cooler canopies, mainly under irrigated conditions, while under drought stress at both Akron and Fort Collins, their canopies were relatively warmer than other cultivars. At both dates, drought stress had a highly significant effect on CTD. CTD of irrigated plots was higher than droughted plots both at anthesis and 21 DAA; however, the magnitude was higher (3.6 ^{0}C) at 21 DAA than at anthesis (1.3 ^{0}C) (Table 20). There was a marked increase in canopy temperature (3.1 ^{0}C) in drought stress plots compare to the irrigated plots (0.8 ^{0}C) over 21 days period, and the cultivars showed greater differences for CTD under drought than irrigated conditions. Pinter et al. (1990) also reported that canopy temperature among genotypes were minimal when plants had adequate soil moisture, but became significant as water became more limited. Blum et al. (1982) reported that as plants with cooler canopies had higher transpiration rate and were capable of relatively higher photosynthesis rate, growth and yield productivity increased compared to other genotypes. However, TAM 107, has a warmer canopy, and may have a lower transpiration rate compare to cooler canopies, and thus conserve water for later critical growth stages. Zipoli et al. (1987) reported that wheat genotypes which had the warmest midday canopy temperature under non-stress conditions also had the lowest water use during vegetative growth stages, and attained, high relative yield when water was limited. TAM 107 has been reported to have tolerance to high temperature stress (Ibrahim and Quick, 2000), which suggests that there might be some other mechanisms (e.g. membrane thermostability) involved that allow photosynthetic activity at high temperatures. The cultivars that had higher biomass were significantly associated with higher CTD measured at anthesis. CTD was significantly associated with GY for both dates of measurement (Table 22). Reynolds et al. (1993) also reported a positive association between the CTD after heading and GY. The association between CTD and days to maturity was significant, which indicates that the late maturing cultivars maintained cooler canopies than the early maturing cultivars on the date of measurement (all cultivars were measured at 21 DAA). This suggests that CTD measurement during the grain filling may be confounded by the maturity differences among the cultivars. There was no significant association between CTD and other variables measured at Akron.

Significant differences among cultivars for chlorophyll content were observed at both dates of measurement at Fort Collins and only at maturity at Akron dryland (Table A12 and A13). The treatments were significantly different only at anthesis at Fort Collins, where chlorophyll content of drought stress was higher than the

Table 20. Mean canopy temperature depression (°C) for nine cultivars grown under irrigated (IR) and dryland (DL) conditions at two locations in 1996.

	Fort Collins				Akron	
	At anthesis		Postanthesis		Dryland	
Cultivar	IR	DL	IR	DL	At anthesis	Post-anthesis
	°C					
Agate	8.9	7.1	7.2	3.9	6.4	5.1
Baca	8.4	6.2	6.7	2.8	6.3	4.9
Lamar	7.8	6.5	6.6	3.8	6.5	5.8
Sandy	8.2	6.4	7.1	3.1	6.3	4.6
Sturdy	7.6	6.2	7.7	4.1	6.4	4.8
TAM 101	7.6	7.0	6.9	3.6	6.6	5.6
TAM 107	6.5	5.8	7.0	2.2	6.7	5.7
TAM 200	7.7	7.0	7.6	4.4	6.7	5.3
Yuma	8.6	7.2	7.4	3.5	6.5	5.5
Mean	7.9	6.6	7.1	3.5	6.5	5.2
LSD (0.05)						
Treatment	0.3		0.3		--	--
Cultivars	1.9		2.0		NS	0.6
T x CV	NS		NS		--	--

NS indicates non-significant.

irrigated treatment (Table 21). Days to flowering was negatively associated with chlorophyll content only when measured at anthesis. Plant height was also negatively associated with chlorophyll contents at both dates of measurement (significant only at Fort Collins) (Table 22). Also certain cultivars (Baca, TAM 101, Yuma) showed an increase in chlorophyll content in response to drought stress at both dates of measurement (Table 21). Baca and TAM 107 exhibited the stay green characteristic to a greater extent, and Sandy also kept green leaves for longer duration than other cultivars (visual observation, data not shown); however, the reading from the chlorophyll meter did not support these observations, except for TAM 107 which also had high chlorophyll content. The chlorophyll meter readings were also not consistent for the cultivars across environments. One possible reason for this inconsistency may be due to random sampling for the two-measurement dates. If the leaves were tagged and chlorophyll was measured on the same leaves within each plot for all the cultivars throughout the growing season, data may be more reliable to draw some meaningful conclusions.

Table 21. Mean chlorophyll contents for nine cultivars grown under irrigated (IR) and dryland (DL) conditions at two locations in 1996.

Cultivar	Fort Collins				Akron	
	At anthesis		Postanthesis		Dryland	
	IR	DL	IR	DL	At anthesis	Post-anthesis
	------------ Chlorophyll meter reading ------------					
Agate	48.7	55.5	54.6	49.7	48.4	51.6
Baca	47.8	52.8	47.6	49.8	47.7	48.0
Lamar	51.7	50.2	47.4	47.0	47.9	49.9
Sandy	51.1	48.7	44.4	41.3	51.1	51.8
Sturdy	53.9	55.0	51.0	49.7	45.6	49.5
TAM 101	54.2	54.9	48.2	50.5	55.2	53.2
TAM 107	52.7	55.3	51.6	49.6	54.8	55.9
TAM 200	54.0	52.0	50.9	45.1	53.9	53.8
Yuma	53.4	54.8	48.7	49.2	53.5	51.5
Mean	52.0	53.2	49.4	48.0	50.9	51.7
LSD (0.05)						
Treatment	0.9		NS		--	--
Cultivar	1.9		3.7		4.8	NS
T x CV	NS		NS		--	--

NS indicates non-significant.

Table 22. Pearson correlation coefficients between grain yield and some physiological traits at Fort Collins, 1996.

	CTD_A[†]	CTD_{PA}[‡]	CHL_A[§]	CHL_{PA}[¶]
CTD_{PA}	0.78**			
CHL_A	-0.34	-0.17		
CHL_{PA}	-0.59*	-0.21	0.57*	
Grain yield	0.63**	0.58**	-0.15	0.25
Biomass	0.66**	0.43	-0.50*	-0.08
Plant height	0.16	-0.08	-0.84**	-0.48*
Anthesis	-0.08	0.17	-0.48*	0.06
Maturity	0.65**	0.82**	-0.36	-0.21

*, **, significant at 0.05 and 0.01 probability levels.

† Canopy temperature depression at anthesis.

‡ Canopy temperature depression at postanthesis.

§ Chlorophyll content at anthesis.

¶ Chlorophyll content at postanthesis.

CHAPTER III

SELECTION FOR DROUGHT TOLERANCE

Introduction

Drought is the major limiting factor to winter wheat (*Triticum aestivum L.*) yield in many parts of the world. Thus improving drought resistance in wheat is one of the objectives in many breeding programs and differences in response to water stress have been found among wheat genotypes (Blum, 1988).

In cereal crops, grain growth is supported by photosynthesis and translocated plant reserves stored mainly in the stem during the pre-anthesis growth stage. Late season drought markedly reduced leaf photosynthesis, and then grain growth primarily depends on the remobilization of the stored reserves from stem (Austin et al., 1980). Genetic variability in remobilization of stored stem NSCs has been reported in cereals (Rawson and Evans, 1971; Blum et al., 1983a).

Chemical desiccants have been used to simulate postanthesis drought stress and to screen genotypes that can support grain growth from stored stem NSCs in the absence of photosynthesis (Nicolas and Turner, 1992; Hossain et al., 1990; Blum et al., 1983b). Selection for larger grains in a spring wheat breeding population treated with chemical desiccant effectively increased grain yield under post-anthesis drought stress with no change in the phenology or plant height, whereas selection without the chemical desiccation treatment did not improve grain filling under postanthesis stress (Blum et al., 1991). Haley and Quick (1993) conducted a similar selection program under chemical desiccation in winter wheat to identify crosses that were tolerant of chemical desiccation.

Two cycles of selection produced F_4 bulks that were more resistant to chemical desiccation stress. These studies showed that the chemical desiccation method may be useful in identifying crosses that are tolerant to postanthesis drought stress. However, reports on how to incorporate this technique into a breeding program are lacking.

Several other techniques have been developed to screen for drought resistance including leaf water potential (Ψ) and relative water content (RWC), and both generally provide a direct measure of water status of plant tissue. Leaf Ψ is a useful measurement in determining the relative water deficits in plant tissues. Martin et al. (1993) while working with wheat concluded that the adaptability of cultivar Sandy (a drought tolerant cultivar) to water limiting environments may be due to its low leaf Ψ maintenance. High grain yield is associated with low leaf Ψ because low Ψ related with maintenance of green leaf tissues (Winter et al., 1988). Variations in leaf Ψ can also be caused by differences in plant height, as taller cultivars maintained lower leaf Ψ than shorter cultivars (Blum and Sullivan, 1997; Kirkham et al., 1978). Leaf RWC was later proposed as a better indicator of water status than Ψ under water stress conditions (Sinclair and Ludlow, 1985). RWC is associated with cell volume, and it may closely reflect the balance between the water supply to the leaf and transpiration rate (Schonfeld et al., 1988). This influences the ability of the plant to recover from stress and consequently affects yield and yield stability (Lilly and Ludlow, 1996). Genetic variability was reported for RWC (Schonfeld et al., 1988) and for leaf Ψ (Winter et al., 1988). There are still discrepancies whether RWC or Ψ has the greater effect on physiological activity and survival of plants.

Knowledge of heritability of a trait is essential during selection since it expresses the breeding value as a guide to the phenotypic value. Traits with high heritabilities can be selected for in early generations while those with poor heritability are selected for in advanced generations. Genetic improvement of drought resistance in crop plants requires identification of relevant physiological stress tolerance mechanisms as selection criteria (Blum, 1988). However, genetic studies of drought tolerance in plants are not abundant. In summary, traits to be incorporated into the selection process for drought tolerance should not only have positive association with yield but should also be heritable.

The objectives of this study were to (i) determine the usefulness of a chemical desiccant to identify the early generation populations tolerant to chemical desiccation, (ii) investigate if differences in Ψ and RWC could be determined among wheat populations under water stress conditions, and (iii) determine the genetic variability and heritability of Ψ and RWC.

Materials and Methods

Three single crosses (Sandy/TAM 107, Sandy/Yuma, and Sandy/Lamar) were made in the greenhouse and advanced to the F_3 generation. Each of the three crosses included the Sandy as the female parent. TAM 107, Lamar, and Yuma were included as male parents. The cultivars vary in yield potential, plant height, maturity, and drought tolerance. In Oct. 1993, 20 F_1 seedlings were vernalized and planted in the greenhouse to obtain the F_2 seed. The 50 F_2 seeds from each of the three crosses were planted at the San Luis Valley research center, in spring 1994 and bulk harvested to obtain F_3 seeds.

Field experiments

Field experiments were conducted at Colorado State University Agricultural Research, Development, and Education Center (ARDEC) on Nunn clay loam (fine, montmorillonitic, mesic Aridic Argiustolls) near Fort Collins, CO during the 1995-96 (1996) and1996-97 (1997) growing seasons.

The F_2 and F_3 unselected bulk populations of the three crosses were planted in the 1996 growing season to obtain chemically desiccated F_3 and F_4 seed. The F_2 generation was planted in a two row plot (9.3 m long and 0.3 m apart with a single replication), while the F_3 generation was planted using three replications. The number of days from January 1 to anthesis was recorded when about 50% of spikes in a plot showed exserted anthers in the central one-third of the spike. The plots were treated with chemical desiccant ($NaClO_3$, 2%W/V @

125mL/m), ten days postanthesis, and machine harvested at maturity to obtain F_3 and F_4 seed from each cross.

Selection for high and low kernel weight was done using the divergent mechanical mass selection method (Haley and Quick, 1993), on chemically desiccated populations of each cross within each generation (F_3 and F_4 seed). These populations were evaluated during the 1997 season. Plots for a complete factorial set of treatments were seeded in fall 1996 in a randomized complete block design with four replications and a split plot restriction. Plots were four rows 4.6 m long and 0.3 m apart, seeded at an average density of 130 seeds m^{-2}. Treatments, within each generation, consisted of the factorial combination from (i) three crosses (ii) three kernel weight sub-samples per cross, and (iii) two desiccation treatments. Chemical desiccation injury was determined by planting two plots (for each treatment combination) next to one another within each replication: one was used as control while the other was treated with sodium chlorate ten days postanthesis. Parental cultivars were also planted in the field in adjacent plots, and also included within each replication. Percent desiccation injury was calculated based on the performance of the two adjacent (F_3 and F_4) plots of each main effect treatment combination within each replication.

$$\% \text{ injury} = [(\text{Control} - \text{Desiccated}) / \text{Control}] \times 100$$

At maturity, grain yield (GY) and yield components were determined from the harvested area of 1 m row length from each plot. The samples were air-dried and weight to determine the dry matter yield and then number of spikes (SN) were counted. The number of kernels per spike (KS) and kernel weight (KW) were determined on 15 randomly selected spikes from each plot. Test weight (TW: grain volume weight) was estimated from a small sample (approx. 250 g) of the harvested grain.

Greenhouse experiments

Water relations

The experiments were conducted in spring 1995 and 1996. The experimental material in each generation consisted of bulked seed from three crosses (Sandy/TAM 107; Sandy/Yuma; and Sandy/Lamar) and the four parents.

In spring 1995, F_2 seeds of the three crosses and the four parents were grown in pots under well watered [100% available water(AW)] and two water stress [medium (15% AW) and severe water stress (0% AW)] treatments. In the well watered (WW) treatment, pots were maintained at 100% available soil water, until physiological maturity. In the medium water stress (MWS) treatment, water was withheld starting at late heading and pots were maintained at 15% available water. In the severe water stress treatment (SWS), water was withheld at late heading until the plant started to show visual wilting. The pots were then rewatered and maintained at 100% available water. Each pot was weighed daily and water requirement determined for that particular treatment.

The germinated seeds were vernalized at 2 ^{o}C for eight weeks. The seedlings were transplanted into plastic pots of 13.5 L capacity (27.6 cm wide x 24.5 cm height). Six seedlings per pot were planted and thinned to four. Soil medium was five parts soil: one part peat moss by volume. Each pot was brought to field capacity by adding a predetermined amount of water prior to transplanting seedlings into it. Water amount for treatments was calculated based on the water retention curve (capillary pressure saturation curve) as determined by the Soil Testing Laboratory at Colorado State University.

Leaf Ψ and RWC were measured at anthesis stage on four fully expanded flag leaves for each cultivar per replication. These measurements were taken between 1130-1500 h. Leaf Ψ was measured using a pressure chamber technique (Turner, 1987). RWC was determined on the same pots as water potential. Immediately after cutting, leaves were sealed inside a plastic bag, and placed in a cooler. Fresh weight was determined within 1 h after excision. Turgid weight was obtained after soaking the leaves in distilled water for 16 to 18 h at room temperature. After soaking, leaves were carefully blotted dry with tissue paper prior to determination of turgid weight. Dry weight was obtained after oven drying the leaves for about 72 h at 65 – 70 °C. The RWC was measured using the expression (fresh weight-dry weight/turgid weight-dry weight) x 100. The experiment design was a randomized complete block with four replications. Each experimental unit consisted of a pot with four seedlings.

In 1996, F_3 and $F_{4,}$ generations and four parental cultivars were grown in the greenhouse. Vernalization, experimental design, water treatments and Ψ and RWC measurements procedures were the same as in the 1995 experiment except there were five plants per pot and Ψ and RWC measurements on five fully expanded flag leaves for each cultivar per replication.

Heritability study

This experiment was performed to estimate the heritability of Ψ and RWC from three wheat populations. Three crosses were made in 1993 and advanced to F_3 as described earlier. The F_3 seed were planted under irrigated and dryland plots in fall 1994 at Fort Collins. Plots were four rows 9.3 m long and rows 0.3 m apart, seeded at an average density of 45 seeds m^{-2} (space planted). The experimental design was a randomized complete block with four replications. Because of unusually wet weather throughout 1995 growing season Ψ and RWC data were not recorded for individual plant selection. At maturity, 50 random plants were selected from each cross. These plants were then grown in the greenhouse (GH) to determine the parent-offspring regression.

Fifteen $F_{3:4}$ plants of each cross and four parents were grown under water stress conditions in the greenhouse in 1996. Seedlings were vernalized for eight weeks and planted in 2.5 L pots. Two seedlings per pot were planted and thinned to one. The water stress (10% available water; calculated based on water retention curve) was applied at heading stage. Each pot was weighed daily and water requirement determined for that particular pot. Ψ and RWC were measured for each pot using the procedure described earlier. The pots were arranged in a randomized complete block with three replications. The $F_{3:5}$ seeds from all replications of single $F_{3:4}$ plants were bulked. In 1997 $F_{3:5}$ progeny were grown in pots. The experimental design, water stress application, and Ψ and RWC measurements were the same as in 1996.

Statistical procedure

Statistical analyses were computed using the Statistical Analysis System (SAS; SAS Institute, 1988). Analysis of variance for all measured variables in all experiments (field and greenhouse) was done using the PROC GLM procedure of SAS. Fisher's Protected Least Significant Difference (LSD) was used to compare means for all measured variables. Simple Pearson correlations between treatment means were calculated using the PROC CORR procedure of SAS.

Heritability of Ψ and RWC was estimated using parent-offspring regression (b), and parent-offspring correlation (r) (Smith and Kinman, 1965). Linear regression coefficients were calculated by regressing $F_{3:5}$ progeny means on $F_{3:4}$ parental means. Standard error (SE) for parent-offspring regression was calculated as follows:

$$SE = [((Y_i^2 - (X_iY_i)2 / X_i^2) / (n - 2)X_i^2] / [X_i^2]$$

Parent-offspring correlation (r) estimates phenotypic variation caused by evaluating the two generations in different experiments and is equivalent to parent-offspring regression from data coded in terms of standard deviation units (Frey and Horner, 1957). The approximate standard error for parent-offspring correlation was calculated as follows:

$$SE\ (r) = (1 - r^2) / (n)^{1/2}$$

Results and Discussion

Field experiments

Highly significant ($p \leq 0.01$) differences were observed between the treatments for all the variables measured in both F_3 and F_4 generations, except for SN in F_3 generation (Tables A14 and A15). Significant ($p \leq 0.05$) differences among crosses were observed for desiccation injury (GYI, TWI, KWI, SWI, and KSI) in the F_3 generation (Table A16), while in F_4 desiccation injury was significant only for GYI, KWI, and SWI (Table A17). The TW injury was significant only at ($p \leq 0.09$) in F_4. In the F_3 generation, the Sandy/Lamar cross showed significantly lower desiccation injury than Sandy/TAM 107 and Sandy/Yuma (Table 23), while in the F_4 generation Sandy/TAM 107 showed the lowest desiccation injury (Table 24). Sandy/Yuma was the most sensitive to chemical desiccant in both F_3 and F_4 generations. Selection for KW within the F_2 and F_3 populations had no significant effect on the desiccation tolerance of the respective populations (Tables 23 and 24).

In F_3, highly significant differences were observed only for TW (Table A14). In F_4, highly significant differences were observed for GY, TW, KW, and KS. The cross x desiccant (C x DES) interaction was highly significant for GY, TW, and KS in F_3 and for GY, KW, and KS in F_4. This C x DES interaction was mainly due to the difference in the magnitude of the response to the two treatments. High KW selection in F_3, produced F_4 bulks with significantly

($p \leq 0.05$) greater KW than those selected for low KW or unselected (Table 23). The selection of high KW in F_2 also produced F_3 bulks with greater KW than those selected for low KW or unselected, but was significant only at ($p \leq 0.16$).

Pearson correlation coefficients for the F_3 population showed strong positive association between GY injury and both TW injury and KW injury ($r=0.86^{**}$ and $r=0.87^{**}$, respectively) and between KW injury and TW injury ($r=0.91^{**}$) as reported from others (Haley and Quick, 1994; Hossain et al., 1990; Blum et al., 1983a,b). GY injury was also strongly associated with SW injury ($r=0.91^{**}$) and KS injury ($r=0.79^{**}$). Control GY was associated with GY injury ($r=0.67^{*}$) and TW injury ($r=0.60$, significant at $p \leq 0.08$).

In the F_4 population, strong positive association was observed between GY injury and TW injury ($r=0.85^{**}$). The correlations between GY injury and KW injury and between TW injury and KW injury were not significant.

Grain filling was markedly reduced by chemical desiccation and caused reduction in GY and its components to a greater extent than was expected particularly in the F_4 generation. The higher desiccation injury than expected was not only due to the reduced grain filling caused by chemical desiccant application, but may also be a limitation in the capacity of the grain to accumulate carbohydrates translocated from stored reserves. The cool, cloudy and rainy weather near anthesis and post anthesis, may have contributed to greater sink limitation through reduced grain endosperm cell division rate, reduced endosperm cell number, and thus a reduction in the dry matter accumulation capacity during the grain filling stage (Sofield et al., 1977).

Table 23. Means of F_3 populations for variables measured at Fort Collins, 1997.

Main effect	Grain yield ($g\ m^{-2}$)	Test weight ($g\ m^{-3}$)	Kernel weight (mg)	Kernels spike^{-1}	Kernel wt. spike^{-1}(g)
Cross					
Sandy/Lamar	467.4 a†	635.7 b	27.1 a	25.0 a	0.71 a
Sandy/TAM 107	456.6 a	678.0 a	26.9 a	26.2 a	0.71 a
Sandy/Yuma	422.9 a	614.3 c	25.7 a	23.6 a	0.64 a
Kernel weight					
Unselected	453.4 a	641.5 a	26.1 a	25.3 a	0.70 a
High KW	452.6 a	645.7 a	27.6 a	24.8 a	0.71 a
Low KW	440.9 a	640.9 a	26.0 a	24.8 a	0.65 a

† Within main effect, means within a column followed by the different letter are significantly different by Fisher's Protected Least Significant Difference (LSD) test (α=0.05).

Table 24. Means of F_3 populations for percent injury of variables measured at Fort Collins, 1997.

Main effect	Grain yield injury	Test weight injury	Kernel weight injury	Kernels spike^{-1} injury	Kernel wt. spike^{-1} injury
	---	---	% injury‡	---	---
Cross					
Sandy/Lamar	45.8 ab†	21.6 b	50.1 ab	29.1 a	63.3 ab
Sandy/TAM 107	41.7 b	12.4 c	40.0 b	6.1 b	45.0 b
Sandy/Yuma	53.1 a	28.5 a	59.5 a	38.4 a	73.4 a
Kernel weight					
Unselected	49.1 a	21.8 a	50.1 a	26.1 a	60.7 a
High KW	44.8 a	19.9 a	49.8 a	24.0 a	58.4 a
Low KW	46.7 a	21.4 a	51.7 a	23.4 a	62.6 a

† .Within main effect, means within a column followed by the different letter are significantly different by Fisher's Protected Least Significant Difference (LSD) test (α=0.05).

‡ Calculated as % injury = (Control-desiccated) / Control x 100 for each desiccation injury variable

Table 25. Means of F_4 populations for variables measured at Fort Collins, 1997.

Main effect	Grain yield ($g\ m^{-2}$)	Test weight ($g\ m^{-3}$)	Kernel weight (mg)	Kernels spike^{-1}	Kernel wt. spike^{-1}(g)
Cross					
Sandy/Lamar	461.1 a†	673.5 a	28.2 a	26.2 a	0.73 a
Sandy/TAM 107	442.8 a	638.7 b	25.9 b	21.1 b	0.60 b
Sandy/Yuma	453.2 a	641.8 b	26.7 b	23.6 ab	0.71 ab
Kernel weight					
Unselected	440.4 a	652.7 a	26.2 b	22.4 a	0.63 a
High KW	472.8 a	656.7 a	27.9 ab	24.2 a	0.74 a
Low KW	443.9 a	644.6 a	26.8 a	24.2 a	0.68 a

† Within main effect, means within a column followed by the different letter are significantly different by Fisher's Protected Least Significant Difference (LSD) test (α=0.05).

Table 26. Means of F_4 populations for percent injury of variables measured at Fort Collins, 1997.

Main effect	Grain yield injury	Test weight injury	Kernel weight injury	Kernels spike^{-1} injury	Kernel wt. spike^{-1} injury
		% injury‡			
Cross					
Sandy/Lamar	57.4 b†	14.1 a	37.4 b	8.0 a	44.7 b
Sandy/TAM 107	71.4 a	19.7 a	49.1 a	30.0 a	66.6 a
Sandy/Yuma	73.4 a	20.3 a	48.1 a	35.0 a	62.6 a
Kernel weight					
Unselected	70.4 a	18.8 a	46.9 a	33.5 a	65.0 a
High KW	64.0 a	17.3 a	45.8 a	12.5 a	57.9 a
Low KW	68.1 a	18.2 a	41.9 a	27.1 a	51.0 a

† Within main effect, means within a column followed by the different letter are significantly different by Fisher's Protected Least Significant Difference (LSD) test (α=0.05).

‡ Calculated as % injury = (Control-desiccated) / Control x 100 for each desiccation injury variable.

Table 27. Means of the parental cultivars for variables measured at Fort Collins, 1997.

Cultivar	Grain yield ($g\ m^{-2}$)	Test weight ($g\ m^{-3}$)	Kernel weight (mg)	Kernels spike^{-1}	Kernel wt. spike^{-1}(g)
Lamar	533 a†	691 a	31.3 a	0.87 a	27.9 a
Sandy	414 b	642 b	23.7 b	0.60 b	27.4 a
TAM 107	465 ab	666 ab	31.5 a	0.82 b	25.7 a
Yuma	547 a	691 ab	31.1 a	0.86 a	24.1 a

† Within main effect, means within a column followed by the different letter are significantly different by Fisher's Protected Least Significant Difference (LSD) test (α=0.05).

Table 28. Means of the parental cultivars for percent injury of variables measured at Fort Collins, 1997.

Cultivar	Grain yield injury	Test weight injury	Kernel weight injury	Kernel wt. spike^{-1} injury	Kernels spike^{-1} injury
	------------------------	------------	% injury ‡	------------	------------------------
Lamar	39.9 b†	19.3 a	35.3 ab	35.6 b	1.0 a
Sandy	73.9 a	11.6 b	46.3 a	63.0 a	29.4 a
TAM 107	53.8 ab	11.1 b	35.7 ab	48.2 ab	19.8 a
Yuma	42.4 ab	9.6 b	29.3 b	32.1 b	5.0 a

† Within main effect, means within a column followed by the different letter are significantly different by Fisher's Protected Least Significant Difference (LSD) test (α=0.05).

‡ Calculated as % injury = (Control-desiccated) / Control x 100 for each desiccation injury variable.

The objective of this study was to assess the utility of the chemical desiccation method, in conjunction with early generation bulk population handling and advance. Significant differences among crosses were observed in the F_3 and F_4 generations. However, the responses of the crosses were not consistent across generation and desiccation injuries were also much higher, particularly in the F_4 generation. The response of the crosses appears to be related to parental response. Sandy was the common parent in all the crosses and the most susceptible to desiccation injury, which may also be a cause of higher desiccation injury to the F_4 generation. The desiccation tolerance of the crosses for GY and KW were not improved by KW selection either in F_2 and F_3 generations, as only one cycle of selection was applied for KW selection which may not be sufficient to improve the desiccation tolerance. Blum et al. (1991) and Haley and Quick (1993) reported that one cycle of selection might not improve the desiccation tolerance in early generation populations. Blum et al. (1991) also observed in some materials that one cycle of selection (not necessarily the first cycle) was sufficient.

Greenhouse experiments

Water relations

Water potential and RWC were studied over two years (1995 and 1996) in three crosses. Each of the three crosses included Sandy as the female parent. TAM 107, Lamar, and Yuma were included as male parents. Mean squares for F_2, F_3, and F_4 are presented in Tables A18 and A19 and for parental cultivars in

Table A20. The treatments were significantly different ($p\leq0.01$) for Ψ and RWC in F_2, F_3, and F_4 generations in both years.

The parental cultivars were highly significantly different for RWC in both years. Ψ was highly significant in 1996, while in 1995 the parental cultivars were significant for Ψ only at ($p\leq0.11$) (Table A20). Sandy had consistently lower Ψ, while TAM 107 maintained higher Ψ and RWC under all water treatments (Tables 33 and 34). Sandy also showed lower RWC compared to other cultivars, but the response was not consistent. Other workers also reported that Sandy consistently had lower Ψ (Morgan et al., 1993; Martin et al.,1993; Morgan and LeCain, 1991). The high and low Ψ and RWC of Sandy and TAM 107 could be attributed to their canopy height (Blum and Sullivan, 1997; Morgan et al., 1993; Kirkham et al., 1978). However, Yuma is a semidwarf cultivar and occasionally showed lower Ψ and RWC both under well watered and water stress conditions. Similarly, Lamar, a tall cultivar, sowed relatively high Ψ and RWC particularly under well-watered conditions (Table 33 and 34).

In the F_2 generation, Ψ and RWC among crosses were not significant within the water stress treatments, but both Ψ and RWC declined with increasing water stress. The Ψ and RWC decreased from -1.92 Mpa and 88.5% in the well-watered (control) to -2.58 Mpa and 74.3% in the severe water stressed treatment, respectively (Table 29).

In the F_3 generation (grown in 1995 and 1996), treatment effects were highly significant ($p\leq0.01$) (Tables A19 and A20). In both years, the moderate stress treatment did not significantly reduce the Ψ and RWC of the F_3 generation compared to the control treatment. The RWC for the three crosses in 1995 ranged from 86.0 to 89.7% in the control and from 83.6 to 88.4% under severe stress conditions. In 1996, the RWC ranged from 85.1 to 86.7% in the control and from 76.2 to 82.6% under severe water stress conditions. The leaf Ψ for the crosses in 1995 ranged from -1.78 to -1.98 Mpa in the control and from -2.03 to -2.28 Mpa under severe water stress conditions. In 1996 the Ψ ranged from -1.91 to -1.99 Mpa in the control and from -2.29 to -2.39 Mpa in severe water stress conditions (Tables 30 and 31). Crosses in the F_3 generation, were highly significant ($p \leq 0.05$) for RWC in both years, while no significant differences were found among crosses in F_3 generation for Ψ in both years (Tables 30 and 31). The crosses showed variation for RWC under both the control and water stress conditions, but the magnitude of differences among crosses was greater under severe water stress. The most consistent genotypic response was observed for Sandy/TAM 107, and it maintained significantly higher RWC than the other crosses under all the water treatments in the F_3 generation in both years. The RWC of Sandy/Lamar was higher or equal to Sandy/Yuma under well-watered conditions; however, under water stress the RWC of Sandy/Lamar declined significantly lower than that of Sandy/Yuma (Tables 30 and 31). The Ψ of the three crosses was the same in the F_3 generation in both years. Treatment and cross interaction was significant only for Ψ in 1996, mainly due to the change in ranking of crosses in response to water stress.

Analyses of F_4 generation (grown in 1996) revealed similar trends as in F_3 generation; both Ψ and RWC was significantly decreased with increasing water

Table 29. Means for water potential and relative water content (RWC) of F_2 populations under three water treatments in the greenhouse, 1995.

	Water potential			RWC		
Cross	Control	MS†	SS‡	Control	MS	SS
	--------Mpa-------			-------- % -------		
Sandy/Lamar	-1.95	-2.15	-2.68	89.9	86.0	76.6
Sandy/TAM 107	-1.85	-2.02	-2.60	87.8	88.0	76.2
Sandy/Yuma	-1.95	-2.00	-2.45	87.9	88.8	70.0
Mean	-1.92	-2.06	-2.58	88.5	87.6	74.3
LSD (0.05)						
Cross		NS			NS	
Treatment		0.2			6	

NS indicates non-significant.
† Moderate water stress.
‡ Severe water stress.

Table 30. Means for water potential and relative water content (RWC) of F_3 populations under three water treatments in the greenhouse, 1995.

	Water potential			RWC		
Cross	Control	MS†	SS‡	Control	MS	SS
	--------Mpa-------			-------- % -------		
Sandy/Lamar	-1.78	-1.88	-2.28	88.3	87.5	83.6
Sandy/TAM 107	-1.90	-1.95	-2.03	89.7	89.2	88.4
Sandy/Yuma	-1.98	-1.80	-2.13	86.0	86.6	84.2
Mean	-1.89	-1.88	-2.15	88.0	87.8	85.4
LSD (0.05)						
Cross		NS			2	
Treatment		0.1			2	

NS indicates non-significant.
† Moderate water stress.
‡ Sever water stress.

Table 31. Means for water potential and relative water content (RWC) of F_3 populations under three water treatments in the greenhouse, 1996.

Cross	Water potential			RWC		
	Control	MS[†]	SS[‡]	Control	MS	SS
	--------Mpa-------			-------- % -------		
Sandy/Lamar	-1.91	-2.19	-2.39	85.3	83.1	76.2
Sandy/TAM 107	-1.99	-2.17	-2.29	86.7	86.3	82.6
Sandy/Yuma	-1.92	-2.23	-2.32	85.1	83.1	78.0
Mean	-1.94	-2.20	-2.33	85.7	84.2	78.9
LSD (0.05)						
Cross		NS			1.5	
Treatment		0.1			1.5	

NS indicates non-significant.
† Moderate water stress.
‡ Severe water stress.

Table 32. Means for water potential and relative water content (RWC) of F_4 populations under three water treatments in the greenhouse, 1996.

Cross	Water potential			RWC		
	Control	MS[†]	SS[‡]	Control	MS	SS
	--------Mpa-------			-------- % -------		
Sandy/Lamar	-1.93	-2.21	-2.26	86.7	82.8	75.2
Sandy/TAM 107	-1.96	-2.10	-2.17	88.1	85.5	78.7
Sandy/Yuma	-1.93	-2.20	-2.21	86.2	82.8	76.6
Mean	-1.94	-2.17	-2.21	87.0	83.7	76.8
LSD (0.05)						
Cross		NS			2	
Treatment		0.1			2	

NS indicates non-significant.
† Moderate water stress.
‡ Severe water stress.

Table 33. Means for water potential and relative water content (RWC) of parental cultivars under three water treatments in the greenhouse, 1996.

	Water potential			RWC		
Cultivar	Control	MS†	SS‡	Control	MS	SS
		--------Mpa-------			-------- % -------	
Lamar	-1.87	-1.98	-2.31	86.4	84.5	73.5
Sandy	-2.09	-2.35	-2.48	84.8	83.1	72.4
TAM 107	-1.85	-2.11	-2.18	87.6	85.3	84.1
Yuma	-1.85	-2.10	-2.25	88.0	85.5	73.7
Mean	-1.92	-2.14	-2.31	86.7	84.6	75.9
LSD (0.05)						
Cultivar		0.1			1.6	
Treatment		0.1			1.4	

† Moderate water stress.
‡ Severe water stress.

Table 34. Means for water potential and relative water content (RWC) of parental cultivars under three water treatments in the greenhouse, 1995.

	Water potential			RWC		
Cultivar	Control	MS†	SS‡	Control	MS	SS
		--------Mpa-------			-------- % -------	
Lamar	-1.83	-1.90	-2.25	89.3	89.6	76.3
Sandy	-1.90	-2.13	-2.40	89.4	90.0	78.3
TAM 107	-1.88	-1.85	-2.00	90.6	91.9	89.7
Yuma	-1.95	-2.00	-2.30	85.5	88.8	71.8
Mean	-1.89	-1.97	-2.24	88.7	90.1	79.0
LSD (0.05)						
Cultivar		NS			5	
Treatment		0.2			4	

NS indicates non-significant.
† Moderate water stress.
‡ Severe water stress.

stress. The crosses were significantly different only for RWC (Table 32). Sandy/TAM 107 showed significantly higher RWC under well watered and water stress treatments. The reduction in RWC in response to water stress was higher in Sandy/Lamar (13.3%) compared to Sandy/Yuma (11.1%) and Sandy/TAM 107 (10.6%). A similar trend among crosses was observed for Ψ, although the crosses were not significantly different.

Heritability study

Heritability of Ψ and RWC was studied in three crosses. Means of Ψ and RWC for F_4 and F_5 generations are presented in Table 35. The crosses were significantly different both in F_4 and F_5 generations for Ψ and only in F_5 generation for RWC. The crosses exhibited wide variation for both traits. Ψ values range from -2.13 to -3.10 Mpa in Sandy/Lamar, -2.15 to -2.87 Mpa in Sandy/TAM 107, and from -1.97 to -3.50 Mpa in Sandy/Yuma. RWC values ranged from 76.5 to 92.1% in Sandy/Lamar, 78.9 to 88.2% in Sandy/TAM 107, and from 78.2 to 92.1% in Sandy/Yuma. The F_4 and F_5 progeny means were usually intermediate between the two parents, except that Sandy/TAM 107 was lower than the parental cultivars for RWC. The cross Sandy/TAM 107 had significantly higher Ψ and RWC than the other two crosses. The parents of this cross also had the largest difference in Ψ and RWC compared with the parents of the other two crosses. However, the Sandy/TAM107 cross progeny did not exhibit a wider range in Ψ and RWC than the other two crosses.

Heritability was measured by parent-offspring regression (b) and parent-offspring correlation (r) using F_4 plants and their F_5 family means. Estimates of heritability for Ψ and RWC varied among crosses. Parent-offspring regression and parent-offspring correlation generally gave similar heritability estimates. Parent-offspring regression heritability was low (0.01-0.27) for Ψ (Table 36) and low to intermediate (0.01-0.45) for RWC (Table 37). Parent-offspring correlation heritability was low to moderately high for Ψ (0.02 - 0.68) and RWC (0.01 - 0.59) (Tables 36 and 37, respectively). Sandy /TAM 107 showed relatively higher heritability than the other two crosses. The response of the crosses generally resembled the parental response. Sandy and TAM 107 were the most different parental pair, e.g., Sandy significantly maintained lower water potential and moderately high RWC, while TAM 107 had both higher Ψ and RWC. Schonfeld et al. (1988) also reported intermediate heritability for RWC. The low heritability for these traits indicates that relatively small genetic effects and/or considerable environmental effects were involved. RWC showed higher heritability than Ψ. The low to intermediate heritability for these traits suggests that progress may be made if the selection was applied in more advanced generations (F_4-F_6), and in a large population, that may provide some transgressive segregate.

Pearson correlation coefficients between the Ψ and RWC were calculated in both F_4 and F_5 generations (Table 38). The association between the two traits was generally not significant. In one case, there was a significant negative association between Ψ and RWC, which suggests that high RWC related to more negative Ψ. Since Ψ and RWC were not correlated, it is possible to perform selection for both traits simultaneously or separately for increasing drought tolerance in winter wheat.

Table 35. Means for water potential (Ψ) and relative water content (RWC) in F_4 and F_5 generations.

Cross	Ψ		RWC	
	F_4 generation	F_5 generation	F_4 generation	F_5 generation
Sandy/Lamar	-2.58 a	-2.66 a	84.6 a	82.7 a
Sandy/Yuma	-2.51 a	-2.59 ab	84.8 a	83.3 ab
Sandy/TAM107	-2.40 b	-2.47 b	85.1 a	84.9 b

† Means followed by the same letter with a column are not significant at (α=0.05) probability level by Fisher's LSD test.

Table 36. Estimates of heritability for water potential (Ψ), using parent-offspring regression (b) and parent-offspring correlation (r), calculated from F_4 plants and their F_5 families.

		Heritability estimates (Ψ)	
Cross	n	b	r
Sandy / Lamar	15	0.10 ± 0.12 †	0.22
Sandy / Yuma	15	0.01 ± 0.10	0.02
Sandy / TAM107	15	0.27 ± 0.09	0.68

† Mean ± SE

Table 37. Estimates of heritability for relative water content (RWC), using parent-offspring regression (b) and parent-offspring correlation (r), calculated from F_4 plants and their F_5 families.

		Heritability estimates (RWC)	
Cross	n	b	r
Sandy / Lamar	15	0.04 ± 0.10 †	0.10
Sandy / Yuma	15	0.01 ± 0.12	0.01
Sandy / TAM107	15	0.45 ± 0.18	0.59

† Mean ± SE

Table 38. Pearson correlation coefficients between water potential (Ψ) and relative water content (RWC) in F_4 and F_5 generations.

Cross	Number of Plants	F_4 generation	F_5 generation
Sandy/Lamar	15	-0.29 NS[†]	-0.12 NS
Sandy/Yuma	15	-0.32 NS	-0.02 NS
Sandy/TAM 107	15	-0.57*	-0.39 NS

* Significant at 0.05 probability level.

† NS indicates non-significant.

SUMMARY

The first portion of these studies was conducted to evaluate the chemical desiccant method, water relations, canopy temperature depression, and leaf chlorophyll content techniques for screening wheat cultivars for drought tolerance. The cultivars were significantly different for chemical desiccation injury. Cultivars with stable kernel weight across environments generally suffered less desiccation injury in the field trials. Grain yield and kernel weight were the most sensitive traits to both chemical desiccation and drought stress; however, chemical desiccation caused significantly higher reduction than drought stress in both the field and greenhouse. There was no association between drought stress and chemical desiccation stress over two years in the field. The ranking of the cultivars was consistent in both years of study under chemical desiccation, but not under drought stress. Thus, the chemical desiccant effects were more repeatable than drought stress effects because desiccant reduced some of the fluctuations caused by natural stress conditions. The magnitude of desiccation injury was similar in the field and greenhouse; however, the ranking of some cultivars was different. The correlations between the field and greenhouse desiccation injuries were also low and nonsignificant for grain yield and kernel weight. Further studies may be needed to explore the opportunity to utilize chemical desiccants in the greenhouse, particularly for the desiccant concentration and mode of application. Cultivar differences were detected for Ψ

and RWC only under water stress conditions, while for CTD and chlorophyll content, cultivars showed differences under both irrigated and dryland conditions. Chlorophyll content may not be suitable as a screening technique as indicated by its inconsistent results for date of measurement and between treatments. Further research may be needed to determine If the chlorophyll content measured on the selected leaves throughout the growing season, would provide consistent results. Similarly, the interpretation of CTD differences among cultivars was difficult. Differences among cultivars in CTD were not only because of different plant water status, but may also be due to other factors including solar radiation, ambient air temperature and humidity, wind speed, and plant and canopy architectural development.

The application of the chemical desiccation method to early-generation bulk populations did not consistently differentiate among the crosses. The desiccation injury was also much higher in the F_4 generation, perhaps due to the deleterious effect of the desiccant on grain growth. The results obtained in these studies suggest further evaluation of chemical desiccation, particularly more diluted concentrations and time of application, to induce a more gradual stress, which could enable identification of desiccant methodology more representative of typical natural postanthesis drought stress. In addition, there is a need to study whether desiccants will induce detrimental effects on assimilation, translocation, and the grain quality of wheat.

Water potential and RWC were studied in three crosses in early-generation unselected bulks and their parental cultivars. The parental cultivars were significantly different for both Ψ and RWC. The heritability estimates were also measured for Ψ and RWC by parent-offspring regression (b) and parent-offspring correlation (r) between F_4 plants and their F_5 progeny means. Parent-offspring correlations gave relatively higher heritability estimates than parent-offspring regressions, particularly for Ψ. Parent-offspring heritability was low (0.01-0.27) for Ψ and low to intermediate (0.01-0.45) for RWC. Parent-offspring correlation heritability was low to moderately high for Ψ (0.02-0.68) and for RWC (0.01-0.59). The low heritability of these traits indicates relatively small genetic effects and/or considerable environmental effects were involved. In the unselected early generation bulk populations, the crosses showed significant differences for RWC, while the crosses were the same for Ψ. This suggests that the progeny selection method would be more beneficial in a breeding program than the bulk selection method for Ψ. The low to intermediate heritability of these traits also suggests that progress may be made if selection is applied in more advanced generations; in large breeding populations, that may provide some transgressive segregates. The correlations between Ψ and RWC were not significant in most cases, indicating that these traits are not genetically or physiologically associated. This suggests that selection for these traits can be done simultaneously or individually for enhancing the level of drought tolerance in wheat. Sufficient genetic variability and heritability of these traits exist to warrant some progress from selection. However, the experimental evidence that selection for these traits in actual breeding programs will lead to superior performance of wheat genotypes in dry environments is lacking.

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APPENDICES

Table A1. Year of release, origin, height, and maturity classification of nine hard red winter wheat cultivars.

Cultivar	Year of Release	Origin	Height	Maturity
Agate	1979	Nebraska	Tall	Late
Baca	1973	Colorado	Tall	Medium
Lamar	1988	Colorado	Tall	Medium-Late
Sandy	1980	Colorado	Tall	Late
Sturdy	1967	Texas	Semidwarf	Medium
TAM 101	1974	Texas	Semidwarf	Early
TAM 107	1987	Texas	Semidwarf	Early
TAM 200	1988	Texas	Semidwarf	Early
Yuma	1991	Colorado	Semidwarf	Medium

Table A2. Mean squares for traits measured under irrigated and dryland conditions at Fort Collins over two years, 1996 and 1997.

Source	df	Biomass	Spike number	Grain yield	Test weight	Kernel weight	Kernels spike^{-1}	Kernel wt. Spike^{-1}	Harvest index	Kernel number*10^{5}
Year (YR)	1	305719***	270	532	4532**	8	1506***	4.60***	0.147***	13
Reps/YR	6	5473	1167	919	347***	14	24	0.04*	0.007***	63
Environment (E)	1	78727***	3074	107011***	5892**	1745***	126*	0.75***	0.263***	194*
YR x E	1	6170	19601***	4553*	1926***	717***	21	0.06*	0.002	396**
E x Rep/YR	6	2418	73	1373	339	25	11	0.02	0.005**	98
Cultivar (CV)	8	16844***	6717***	2383**	446***	284***	135***	0.17***	0.008***	892***
YR x CV	8	3258	1870*	893	152**	4	20	0.03*	0.003	67
E x CV	8	7406*	987	2467**	135*	12	19	0.04**	0.004**	36
YR x E x CV	8	2142	99	745	69	5	18	0.02	0.004**	75
Error	96	3675	896	873	54	7	11	0.01	0.002	57

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

Table A3. Mean squares for variables measured at Akron over two years, 1996 and 1997.

Source	df	Biomass	Spike number	Grain yield	Test weight	Kernel weight	Kernels spike^{-1}	Kernel wt. Spike^{-1}	Harvest index	Kernel Number*10^{5}
Year (YR)	1	343658***	1876	66638***	1797***	968***	849.7***	3.520	0.0100***	1023***
Rep/YR	5	2687	791	502	12	19	19.2	0.033***	0.0003	42
Cultivar (CV)	8	5188	1501	1588**	75**	68***	65.7**	0.051**	0.0040***	184**
YR x CV	8	4869	874	702	62**	8	2.6	0.009	0.0020***	48*
Error	40	2512	635	410	20	9	12.7	0.017	0.0003	22

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

Table A4. Mean squares for traits measured under irrigation without (control) and with chemical desiccant (DES) at Fort Collins over two years, 1996 and 1997.

Source	df	Biomass	Spike number	Grain yield	Test weight	Kernel weight	Kernels spike^{-1}	Kernel wt. Spike^{-1}	Harvest index	Kernel number*10^5
Year (YR)	1	175770**	4273	1296	2074	91	1628***	0.056**	0.056*	584*
Reps/YR	6	8242*	1274	905	454***	31**	26	0.005	0.005	143
Desiccant (DES)	1	472198***	1033	261819***	10668***	4052***	318***	0.302***	0.302***	1791***
YR x DES	1	3315	7568**	6504**	509**	222***	42	0.038***	0.038**	3
Error a	6	3187	1044	2244	185	14	9	0.007	0.007	86
Cultivars (CV)	8	25784***	7196***	2986**	345***	247***	208***	0.009***	0.009***	608***
YR x CV	8	3680	2991**	1166	97*	8	22	0.004*	0.004*	156
CV x DES	8	3141	1013	2657**	161**	15	29	0.005**	0.005**	65
YR x CV x DES	8	2072	553	897	76	4	6	0.002	0.002	64
Error b	96	3320	933	1042	48	9	13	0.002	0.002	78

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

Table A5. Mean squares for desiccation injury of traits measured at Fort Collins over two years, 1996 and 1997.

Source	df	Biomass injury	Grain yield injury	Test weight injury	Kernel weight injury	Kernel number injury	Harvest index injury	Kernels per spike injury
Year (YR)	1	334**	2155**	181***	3056***	140	5889***	725
Rep/YR	6	117	630	55***	219	561	1112***	157
Cultivar (CV)	8	190	595*	80***	437**	441	608*	579
YR x CV	8	183	279	44*	45	308	242	167
Error	47	121	298	11	123	648	242	370

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

Table A6. Mean squares for traits measured under irrigation treated with chemical desiccant and dryland conditions at Fort Collins over two years, 1996 and 1997.

Source	df	Biomass	Spike number	Grain yield	Test weight	Kernel weight	Kernels spike^{-1}	Kernel wt. spike^{-1}	Harvest index	Kernel number*10^{3}
Year (YR)	1	249633***	4592*	11372***	7924***	321***	2018***	4.62***	0.035***	31
Reps/YR	6	9751**	642	1120	48*	6	21	0.04*	0.001	136
Stress (S)	1	155579***	413	31364***	792***	505***	43*	0.74***	0.001	1863***
YR x S	1	16539*	2649	275	423***	130***	3	0.06*	0.022***	1018**
E x Rep/YR	6	1712	239	934	25	10	11	0.02	0.001	118
Cultivar (CV)	8	17396***	4856***	6061***	277***	215***	258***	0.17***	0.010***	1261***
YR x CV	8	4756	1493	1157	1 18***	5	24*	0.03*	0.003**	239
CV x S	8	2854	1125	838	26	6	19	0.04**	0.001	201
YR x CV x S	8	1914	779	712	33	3	6	0.01	0.002	160
Error	96	3455	1095	853	20	2	10	0.01	0.001	170

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

Table A7. Mean squares for stress injury caused by desiccant and drought of traits measured at Fort Collins over two years, 1996 and 1997.

Source	df	Biomass injury	Grain yield injury	Test weight injury	Kernel weight injury	Kernel number injury	Harvest index injury	Kernel wt. spike^{-1} injury	Kernels spike^{-1} injury
Year (YR)	1	1936***	1418*	1	35	1053	9027***	150	520
Reps/YR	6	175	848*	19	146	1319*	1094***	254	228
Desiccant (DES)	1	3068***	24606***	1066***	13078***	4380**	17046***	16705***	1172
YR x DES	1	217	519	351***	5229***	2346*	109	6335**	233
E x Rep/YR	6	8082***	224	45***	213	299	245	760**	197
Cultivar (CV)	8	97	462	56***	463***	473	498*	1268***	746*
YR x CV	8	178	385	37***	50	610	334	271	101
CV x DES	8	207	347	34***	122	377	233	164	182
YR x CV x DES	8	92	199	21*	56	370	220	222	209
Error	96	150	331	9	109	591	217	271	330

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

Table A8. Mean squares for variables measured in the greenhouse, 1996.

Source	df	Biomass	Spikes number	Grain yield	Kernel weight	Kernels spike^{-1}	Kernel wt. spike^{-1}
Rep	3	13	8	5	0.03	13	0.02
Treatment (T)	2	688***	89***	277***	2.47***	9	1.46***
Cultivar (CV)	8	277***	16**	56***	0.23***	182***	0.02***
T x CV	16	19	7	11	0.04***	21	0.04
Error	78	24	5	10	0.01	20	0.03

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

Table A9. Means for biomass and spike number pot^{-1} in the greenhouse,1996.

	Biomass			Number of spikes		
Cultivar	Irrigated	Desiccant	Stress	Irrigated	Desiccant	Stress
	-----------g-----------			---------- no. ---------		
Agate	24.8	19.3	20.8	11.5	11.5	8.5
Baca	24.5	18.3	23.4	12.5	10.0	10.0
Lamar	35.6	18.7	25.6	15.0	9.3	9.5
Sandy	28.0	17.7	26.0	14.0	8.3	10.3
Sturdy	25.6	15.6	22.4	12.0	8.5	9.8
TAM 101	19.3	11.2	14.9	9.8	6.8	7.8
TAM 107	16.7	9.7	14.3	9.8	8.0	8.3
TAM 200	15.6	9.5	13.1	9.5	8.5	8.0
Yuma	24.5	14.8	21.8	13.0	9.0	9.8
Mean	23.8	15.0	20.2	11.8	8.9	9.2
LSD (0.05)	8.5	5.9	6.9	4.5	2.4	2.5

Table A10. Means for kernel spike^{-1} and kernel weight spike^{-1} in the greenhouse,1996.

	Kernels spike^{-1}			Kernel weight spike^{-1}		
Cultivar	Irrigated	Desiccant	Stress	Irrigated	Desiccant	Stress
	----------- no. -----------			---------- g ---------		
Agate	22.9	20.8	22.5	1.03	0.76	1.14
Baca	23.4	23.1	27.3	0.91	0.76	1.08
Lamar	31.6	27.2	25.8	1.39	0.87	1.19
Sandy	26.0	29.7	30.1	1.05	0.78	1.18
Sturdy	26.3	26.1	23.5	0.95	0.77	1.03
TAM 101	17.8	15.9	17.3	0.85	0.60	0.80
TAM 107	19.1	18.4	20.3	0.87	0.49	0.86
TAM 200	27.3	23.3	20.2	1.05	0.41	0.79
Yuma	26.4	25.8	27.1	1.03	0.60	1.14
Mean	24.5	23.4	23.8	1.02	0.67	1.02
LSD (0.05)	4.5	2.4	2.5	7	5.3	6.8

Table A11. Mean squares for water potential (WP) and relative water content (RWC) in the greenhouse, 1996.

Source	df	Water potential	RWC
Rep	3	0.03	25*
Treatment (T)	1	4.29***	50*
Cultivar (CV)	8	0.10**	32**
T x CV	8	0.9**	5
Error	51	0.02	8

*, *** Significant at the 0.05 and 0.001 probability levels, respectively.

Table A12. Mean squares for variables measured at Akron, 1996.

Source	df	WP	RWC	CHL$_A$†	CHL$_{pa}$‡	CTD$_A$§	CTD$_{pa}$¶
Rep	2	2.7	15.5	0.5	2.5	2.83***	0.21
Cultivar	8	1.6	18.8*	16.7	33.6**	0.51**	0.08
Residual	16	0.8	7.2	7.4	4.7	0.10	0.08

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

† Chlorophyll content measured at anthesis.

‡ Chlorophyll content measured during postanthesis.

§ Canopy temperature depression measured at anthesis.

¶ Canopy temperature depression measured during postanthesis.

Table A13. Mean squares for variables measured at Fort Collins, 1996.

Source	df	CHL$_A$†	CHL$_{PA}$‡	CTD$_A$§	CTD$_{PA}$¶
Treatment (T)	1	28.0***	35.0	31.7***	241.2***
Rep/T	6	5.9*	7.1	1.9***	3.0***
Cultivar (CV)	8	47.2***	55.5***	2.3***	1.7***
T x CV	8	3.3*	16.7	0.6	0.9
Error	48	2.3	13.7	0.4	0.4

*, *** Significant at the 0.05, and 0.001 probability levels, respectively.

† Chlorophyll content measured at anthesis.

‡ Chlorophyll content measured during postanthesis.

§ Canopy temperature depression measured at anthesis.

¶ Canopy temperature depression measured during postanthesis.

Table A14. Mean squares of F_3 populations for variables measured at Fort Collins, 1997.

Source	df	Grain yield	Test weight	Kernel weight	Spike number	Kernel wt.spike^{-1}	Kernels spike^{-1}
Reps	2	9300***	165	63***	1087	0.17**	65*
Cross (C)	2	1401	1981***	11	6	0.04	29
Desiccant (DES)	1	368462***	29957***	3560***	5766	4.99***	759***
C x DES	2	8229***	1461***	20	1396	0.12**	112**
KWC	2	127	13	14	611	0.02	2
C x KWC	4	1302	114	6	2050	0.07*	58*
DES x KWC	2	3274*	40	1	4111	0.00	2
C x DES x KWC	4	1082	88	1	2370	0.00	1
Error	34	925	63	7	2487	0.02	18

*, **, *** Significant at 0.05, 0.01, and 0.001 probability levels, respectively.

Table A15. Mean squares of F_4 populations for variables measured at Fort Collins, 1997.

Source	df	Grain yield	Test weight	Kernel weight	Spike number	Kernel wt.spike^{-1}	Kernels spike^{-1}
Reps	2	1006	17	5	2102	0.02	48
Cross (C)	2	219	695***	24**	3227	0.08	117**
Desiccant (DES)	1	428125***	22317***	3304***	31200***	4.46***	541***
C x DES	2	4271**	235	22**	312	0.04	128**
KWC	2	819	73	14*	906	0.05	17
C x KWC	4	1124	29	5	474	0.05	13
DES x KWC	2	226	12	7	1665	0.01	23
C x DES x KWC	4	1131	50	7	2909	0.02	19
Error	34	889	87	4	2324	0.03	26

*, **, *** Significant at 0.05, 0.01, and 0.001 probability levels, respectively.

Table A16. Mean squares for desiccation injury of F_3 populations for variables measured at Fort Collins, 1997.

Source	df	Grain Yield injury	Test weight injury	Kernel weight injury	Kernel wt.spike^{-1} injury	Kernel spike^{-1} injury
Reps	2	159	49	145	65	35
Cross (C)	2	297*	591***	689*	1866*	2491*
KWC	2	41	14	9	40	18
C x KWC	4	10	36	105	87	11
Error	16	67	20	159	382	509

*, *** Significant at 0.05 and 0.001 probability levels, respectively.

Table A17. Mean squares for desiccation injury of F_4 populations for variables measured at Fort Collins, 1997.

Source	df	Grain Yield injury	Test weight injury	Kernel weight injury	Kernel wt.spike^{-1} injury	Kernel spike^{-1} injury
Reps	2	41	5	23	2154**	494
Cross (C)	2	704*	104	375**	1227*	1834
KWC	2	96	5	62	440	1048
C x KWC	4	145	19	95	433	258
Error	16	208	37	50	292	779

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

Table A18. Mean squares for water potential (Ψ) and RWC of F_2 and F_3 populations in the greenhouse, 1995.

		F_2 population		F_3 population	
Source	df	Ψ	RWC	Ψ	RWC
Rep	3	0.02	24	0.02	14
Treatment (T)	2	1.44***	762***	0.28***	25*
Cross (C)	2	0.05	14	0.00	39**
T x C	4	0.02	28	0.06**	4
Error	23	0.07	55	0.01	7

*, **, *** Significant at 0.05, 0.01, and 0.001 probability levels, respectively.

Table A19. Mean squares for water potential (Ψ) and RWC of F_3 and F_4 Populations in the greenhouse, 1996

		F_3 population		F_4 population	
Source	df	Ψ	RWC	Ψ	RWC
Rep	3	0.01	4	0.05	9
Treatment (T)	2	0.46***	154***	0.51***	324***
Cross (C)	2	0.001	47***	0.02	23*
T x C	4	0.01	7	0.03	2
Error	23	0.01	3	0.01	7

*, *** Significant at 0.05 and 0.001 probability levels, respectively.

Table A20. Mean squares for water potential (Ψ) and RWC of parental cultivars in the greenhouse, 1996.

		1995		1996	
Source	df	Ψ	RWC	Ψ	RWC
Rep	3	0.03	41	0.02	12*
Treatment (T)	2	0.54***	552***	0.53***	491***
Cultivar (CV)	3	0.13	170**	0.18***	51***
T x CV	6	0.03	60	0.02	29***
Error	30	0.06	32	0.02	4

*, **, *** Significant at 0.05, 0.01, and 0.001 probability levels, respectively.