DISSERTATION

CHEMICAL DESICCATION TOLERANCE AND NONSTRUCTURAL CARBOHYDRATE DYNAMICS IN WINTER WHEAT

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY TESHOME GIRMA MULAT ENTITLED CHEMICAL DESSICATION TOLERANCE AND NONSTRUCTURAL CARBOHYDRATE DYNAMICS IN WINTER WHEAT BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

CHEMICAL DESICCATION TOLERANCE AND NONSTRUCTURAL CARBOHYDRATE DYNAMICS IN WINTER WHEAT

Winter wheat (*Triticum aestivum* L.) often experiences postanthesis drought stress that causes crop yield and quality losses. Contact chemical desiccants have been proposed as a means of identifying genotypes with improved ability to support grain filling from stem nonstructural carbohydrates (NSC) in the absence of photosynthesis during grain filling. Information on genetic variation in stem NSC, and its remobilization to developing grains under chemical desiccation, is therefore important. The objectives of this study were (1) to characterize chemical desiccation response, dryland yield performance and NSC concentration and remobilization of F_2-derived lines and their parents, (2) determine associations among chemical desiccation injury, dryland performance and NSC measurements, and (3) estimate genotypic variance components of agronomic traits and NSC measurements under chemical desiccation. $F_{2:4}$ lines developed from six crosses between seven parents with contrasting agronomic traits were planted in a split plot with two replications in 1998 and 1999 under irrigation at Fort Collins. Sodium chlorate ($NaClO_3$, 2% W:V, 125 mL m^{-2}) was applied to each subplot 15 d postanthesis. The same lines were also evaluated at four dryland locations (Akron in 1998 and Burlington, Akron, and Walsh in

1999) in a randomized complete block design with two replications. Yield injury from chemical desiccation ranged from 13 to 37% among entries, with reductions in both kernel weight (13 to 23%) and kernel number (8 to 32%). Significant associations were observed between grain yield injury and both biomass injury ($r = 0.65$, $P<0.05$) and control kernel weight ($r = 0.57$, $P<0.05$). Average performance under dryland conditions was less than that observed under chemical desiccation, although test weight was much less in the desiccated treatment compared to the dryland treatment. Grain yield under dryland conditions was not associated with either grain yield injury or kernel weight injury under chemical desiccation. Significant genotypic variance was observed for most traits examined, suggesting that progress in selection may be realized within these populations. Inconsistency among entries for desiccation tolerance, and the lack of correlation between desiccation tolerance and dryland performance, suggest that additional research is necessary to identify strategies and techniques to successfully exploit the chemical desiccation method for applied wheat breeding programs. Nonstructural carbohydrate concentration was determined from stem samplings made at 14 d postanthesis and at maturity in both the control and desiccated subplots. Significant variation among entries was observed for NSC concentration at postanthesis and maturity in both control and desiccated treatments. Very little consistency among entries was observed for NSC measurements across years. Stem NSC concentration at maturity was lower under desiccation than in the control treatment, suggesting that chemical desiccation reduced the source of NSC. Stem NSC concentration at postanthesis

was positively correlated with NSC remobilization during grain filling in the desiccated ($r=0.90$, $P<0.001$) treatment, suggesting that the size of the NSC pool available at the onset at grain filling is important for reserve remobilization. Most correlations among grain yield and yield components, and variables related to stem NSC were not significant. Genetic variance estimates indicated that significant genetic variation for NSC concentration and remobilization was present among the lines tested. Selection within populations that have high genetic variance should provide progress to improve NSC parameters.

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LITERATURE REVIEW

Wheat Developmental Stages

To understand the physiological and ecological aspects of wheat (*Triticum aestivum* L.) yield it is necessary to study the physiology of crop development. The effects of environmental factors on crop growth and yield differ depending upon the developmental stages when these factors act (Fischer, 1985; Thorne and Wood, 1987; Slafer et al., 1994a). Wheat plant development can be described in different stages or phases, which in turn, can be defined in terms of internal (physiological) or external (morphological and anatomical) changes. However, crop development is a continuity of vegetative, reproductive, and grain filling phases through which the crop initiates and grows its organs and completes cycle. The duration of each phase and the number of primordia initiated is determined by genetic and environmental factors, and their interaction (Miralles and Slafer, 1999).

Several authors have described the wheat plant and its development. Some of them have described morphological changes in the apical meristem (Waddington et al., 1983; Gardner et al., 1985) while others have described visible developmental growth stages (Large, 1954; Haun, 1973; Zadoks et al., 1974). Delineation of development into distinct morphological stages allows nondestructive identification of developmental progress but provides no

information about the sequence and timing of events in the shoot apex when development actually occurs (Miralles and Slafer, 1999).

Early vegetative growth, including initiation of roots, leaves, and stems, occurs during the first stage between emergence and floral initiation. Both genetic and environmental factors have been shown to affect the rate of leaf appearance. Syme (1974) concluded that semidwarf wheat cultivars produce leaves more quickly than standard height cultivars. Effects of environmental conditions on rate of leaf appearance are evident when crops are grown at different dates and locations (Baker et al., 1980; Kirby and Perry, 1987; Stapper and Fischer, 1990). Winter wheat is sown in the fall and early vegetative growth begins during cool, short days under relatively low radiation levels. This vegetative growth is important to crop canopy development and maximization of solar radiation interception. The relation between light interception and net canopy assimilation depends on canopy architecture (Evans et al., 1975) and leaf area index (LAI) (Hay and Walker, 1987). The LAI of a typical wheat canopy reaches a peak prior to anthesis and declines with advancing maturity and senescence (Evans et al., 1975). Maximum leaf area per culm is usually reached prior to heading when the flag leaf becomes fully expanded (Simmons, 1987). In many environments, many wheat crops have virtually unlimited resources at the beginning of their growing seasons, however, growth rate increase, soil and water resources becomes limiting, availability becomes limiting. Immediately after resources become limiting, not all the tillers that were potentially expected to appear do so. However, the rate of tiller appearance, though still positive,

gradually decreases from that predicted from potential (Masle, 1985). The availability of adequate resources becomes so limiting that no new tillers appear. The resource is insufficient to maintain growth of all tillers and some die, in the reverse order that they appeared. The rate of leaf production, rate and duration of leaf expansion, extent of tillering, relative survival of tillers, and leaf duration are all important in the development and maintenance of high LAI (Hay and Walker, 1989).

The second growth stage is the period between floral initiation and anthesis. Floral initiation is that point in development at which the shoot apex begins initiation of floral components. Shortly after the initiation of spikelets, floret initiation begins in the spikelets first initiated. Developments begin in lower region of the middle one-third of the spike and continue upward and downward toward both ends of the spike (Miralles and Slafer, 1999). Floret development begins in the basal position of each spikelet and progresses from there toward the distal position (Sibony and Pinthus, 1988). By the time of terminal spikelet initiation, three to five florets are commonly initiated in the central spikelets of the spike. This occurs in response to the inductive conditions of temperature followed by increasing day length.

The timing of reproductive development in wheat is an important determinant of grain yield (Evans et al., 1975). Early inflorescence development leads to increased risk of frost injury while delayed development leads to increased susceptibility to high temperatures or water stress during grain filling. Initiation of the terminal spikelet marks the end of spikelet formation and after this

time no environmental conditions affect spikelet number, although the number of differentiated florets per spikelet may be affected (Evan et al., 1975).

The maximum number of floret primordia per spikelet normally ranges between 6 and 12 (Sibony and Pinthus, 1988; Youssefian et al., 1992), mostly depending on the spikelet position. Usually, only one to four florets complete their development to produce fertile florets (Miralles and Slafer, 1999). The proportion of florets that maintain a normal rate of development after onset of rapid spike and stem growth is related to the availability of assimilates for the growing spike, a function of crop growth during this period (Fischer, 1985; Thorne and Wood, 1987; Savin and Slafer, 1991).

The third major growth stage, the grain filling period, begins with anthesis and ends with physiological maturity. The sequence of fertilization follows the same pattern as spikelet differentiation and floret development across the spike (Rawson and Evans, 1970). The proportion of fertile florets actually producing a 'normal' grain is usually less than 100 %, likely because of competition for assimilates (Savin and Slafer, 1991). Grain filling can be further divided into three distinct phases with respect to dry weight accumulation: an initial lag phase, a period of linear growth, and a log phase (Simmons, 1987). The initial lag phase occurs immediately after anthesis, lasting about 7 to 10 d after anthesis, and is characterized by a period of rapid endosperm cell division and increasing endosperm cell number. The number of endosperm cells formed by a kernel ultimately influences its rate of growth and final weight (Brocklehurst, 1977; Singh and Jenner, 1982, Hay and Walker, 1989). During this phase, which lasts for

about 20 to 30 % of the total postanthesis period (Gebeyehou et al., 1982), most of the endosperm cells are developed and the potential size of the grain is defined. Endospermatic cell formation may continue during part of the subsequent grain growth phase (Miralles and Slafer, 1999). The rate of endosperm cell division and the final cell number are influenced by light intensity, water stress, temperature, and genotype (Brocklehurst, 1977). The duration of the linear phase growth period varies (depending on water stress, temperature, and genotype), usually lasting for 2 to 4 weeks (Martinez-Carrasco and Thorne, 1979; Simmons and Crookston, 1979). Since most of the final weight of the kernel is accumulated during this relatively brief period, it is not surprising that the rate of growth during this time is closely associated with the final weight achieved (Simmons and Crookston, 1979). Reductions in assimilate supply to kernels may result in reduced growth, particularly if reduction occurs early in development (Simmons et al., 1982). The growth and final weight of an individual kernel depends on the spikelet and floret position at which it forms (Rawson and Evans, 1970; Bremner, 1972). Kernels formed in the centrally positioned spikelets and in the proximal florets within an individual spikelet are usually the largest (Simmons, 1987). Decreased rates of grain filling occur during the log phase resulting in grain yields asymptotically approaching their maximum unless grain filling is terminated by an external factor, such as severe water stress (Nicolas et al., 1984) or sudden heat shock (Savin et al., 1996). Final grain weight at harvest is influenced both by the rate of grain growth during the linear phase and duration of the linear phase of grain growth (Sofield et al., 1977).

Drought Stress Effects on the Wheat Plant

Drought stress occurs when the amount and distribution or both of precipitation or irrigation are sufficiently low to cause reduction in crop yield (Hale and Orcutt, 1987). Water deficits occur in plants whenever atmospheric demand exceeds the supply of water from the soil. Water stresses in plants develop as a consequence of water loss from the leaf as the stomata open to allow the uptake of CO_2 from the atmosphere for photosynthesis (Turner, 1986). Physical, physiological, and biochemical effects of water stress depend of the degree and timing of drought conditions in relation to the stage of plant development (Hale and Orcutt, 1987).

The most common dryland cropping system in the Great Plains has been the wheat-fallow rotation, where planting follows a fallow period for soil moisture conservation (Dhuyvetter et al., 1996). Soil moisture stored during the fallow period is often sufficient for pre-anthesis growth and development. The unreliability of precipitation is the main reason that postanthesis drought stress imposes a significant limitation on winter wheat production in the Great Plains. Dhuyvetter et al. (1996) found that between 1991 and 1993, the harvested area of dryland winter wheat in western Kansas, western Nebraska, and eastern Colorado ranged from 2.5 to 2.9 million ha annually.

In a Mediterranean climate, winter cereals grow well during winter and plants grow vigorously as soon as temperatures rise in spring. Precipitation is stored in the soil, which supplies the spring and summer water requirements. Soil water is often inadequate to meet crop water requirements towards maturity and

crops suffer postanthesis water stress (Santibanez, 1994). Estimates suggest that from 70 to 90 % of grain yield is derived from photo-assimilate produced after anthesis (Austin et al., 1977; Bidinger et al., 1977). Water deficits and their effect on physiological processes affecting yield can be examined in terms of their effects on photosynthesis, stomata behavior, respiration and photorespiration, and translocation of assimilate (Begg and Turner, 1976). Grain growth in wheat depends on carbon from three sources: current assimilation, remobilization of assimilates stored in the stem and other plant parts prior to anthesis, and remobilzation of assimilates stored temporarily in the stem after anthesis (Kobata et al., 1992).

Current Photosynthate During Grain Filling

Photosynthesis in plants is reduced under water stress both by reduction in total photosynthetic surface area and by reduction in the rate of photosynthesis per unit area (Fischer, 1973). Reduction of surface area at any stage of the life cycle in wheat, due to reduced cell expansion or cellular division, early senescence, or reduced meristematic initiation, limits photosynthesis, the major source of carbohydrates during grain filling (Fischer, 1973). Judging by the relative photosynthetic activity of various organs during grain filling, the flag leaf blade and spike likely contribute the greatest quantities of photo-assimilate to the grain, with the flag leaf blade responsible for as much as 50 % of the canopy photo-assimilate during early- and mid-grain filling (Rawson et al., 1983). Stem and leaf sheaths account for 39 to 44 % of the canopy photosynthesis in wheat crops (Puckridge, 1969). Toward the end of grain filling, stem and spike

photosynthesis can become the major sources of current photo-assimilate since they tend to remain green after many of the leaves have senesced (Spiertz et al., 1971). During this latter period of grain filling, 20 % of the grain carbohydrate may be supplied by spike photosynthesis (Evans et al., 1975).

The importance of maintaining photosynthetic capacity in the upper leaf blades, sheaths and spike is evident (Evans and Rawson, 1970). Awns can substantially increase spike photosynthetic rate (Evans and Rawson, 1970; Teare et al., 1972). Awns may also be neutral or negative in more humid conditions (McKenzie, 1972).

For winter or spring wheat, the main shoot and early tillers are most likely to complete development and form grain (Simmons, 1987). Late formed tillers often senesce prematurely in a dryland crop environment. Tillers destined to senesce may translocate a portion of their current photo-assimilate directly to surviving shoots before visible signs of senescence are apparent. Despite their potential resource contributions, unproductive tillers may be undesirable (Rawson and Donald, 1969). However, Kobata et al. (1992) found that unproductive tillers provide a source of dry matter for grain filling. Not only is grain filling on the main stem and earliest tillers supported from pre-anthesis assimilates stored in the individual tillers, it is also supported by transfer of dry matter from late formed tillers, even though these late formed tillers may be fertile and set seed.

Austin (1992) indicated that to achieve higher yields it would be necessary to increase leaf photosynthesis. This may be done by increasing radiation interception by the crop during the growing season although this may be dependent on incident radiation and the ability of the crop to intercept it (Slafer et al., 1999). As the main intercepting organs are leaf laminae, the obvious characteristic of interest is LAI. This opportunity exists only when LAI is below critical levels. Under less favorable environments where soil water may be limited or there is a short growing season, rapid early growth of the crop may be critical to promote better performance (Richards, 1996a, 1996b). The possibility of increasing leaf photosynthesis has received considerable attention. The rationale for this research has been that, as almost all dry matter is produced by leaf photosynthesis, it would be expected that increasing this rate would confer greater biomass and yield. It has been reported in wheat that wild, low yielding related species have higher photosynthetic rates than modern, high yielding cultivars (Austin et al., 1982; Johnson et al., 1978; Carver et al., 1989). Deckerd et al. (1985) found no increase in the level of interception of incoming radiation among cultivars and no consistent changes in leaf area between old and new cultivars.

Photorespiration and respiration are affected by water deficits, generally declining with increased level of water stress (Hay and Walker, 1989). Although photorespiration decreases with increasing stress, there is evidence that it declines less than gross photosynthesis, and thus the ratio of photorespiration to gross photosynthesis increases with increasing levels of stress. Together with

the inhibitory effect of Calvin cycle enzymes, this increase in photorespiration relative to gross photosynthesis leads to decreased photosynthetic efficiency and a greater nonstomatal limitation to photosynthesis (Hay and Walker, 1987).

Most dry matter contributing to grain yield is newly assimilated during grain filling. When drought stress occurs, however, current photo-assimilate supplies are reduced and plants must increasingly rely on previously stored assimilate for grain filling (Gallagher et al., 1976). Bidinger et al. (1977) estimated that 13 % of grain yield in a well-watered wheat crop could be attributed to remobilization of assimilates stored pre-anthesis. The contribution increased to 27% under postanthesis drought stress conditions. Wardlaw (1967) studied photosynthesis under water stress and its subsequent effects on carbohydrate translocation and grain growth. He found that water stress reduced flag leaf photosynthesis which was not the result of either 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 tissue (Bidinger et al., 1977). Kobata et al. (1992) demonstrated that grain filling of wheat, which is affected by a high rate of water deficit development, is maintained above that expected from postanthesis dry matter accumulation because remobilization of assimilates to the grain continued despite a reduction in carbon assimilation. In their study, the authors suggested that carbon assimilation, and hence dry matter production, is more affected than remobilization during postanthesis water deficits. Palta et al. (1994) estimated that between anthesis and grain maturity, ^{13}C remobilized to the grain was 35 %

higher in plants growing under rapidly developing water deficits than plants growing under slow-developing water deficits.

Nonstructural Carbohydrates

Photosynthetic activity of wheat flag leaves decreases rapidly when the developing grain reaches about half its final size. After that time, remobilization and spike photosynthesis are the main sources of carbohydrate for grain filling (Wardlaw and Porter, 1967; Hunt, 1978; Frederick, 1997). Stems of cereal grains, including wheat, accumulate non-structural carbohydrates (NSCs) near anthesis, and they nearly disappear by maturity (McCaig and Clarke, 1982; Frederick and Bauer, 1999). These NSCs are mainly in the form of oligosaccharides and fructans, both short chain carbohydrates (McCaig and Clarke, 1982). Fructans, the most abundant stem NSC component, account for up to two-thirds of total NSC and almost one-third of the stem dry weight at anthesis (McCaig and Clark, 1982; Hendrix et al., 1986).

Hunt (1978) reported that winter wheat cultivars showed an increase in stem weight for 14 to 21 d after spike emergence. NSCs have been the major chemical component associated with these changes in stem dry weight during grain filling (Wardlaw, 1968; Evans and Rawson, 1970; Rawson and Evans, 1971). Assimilate supply for grain growth comes 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) showed that NSCs stored in the stem (mostly in the top two internodes) prior to anthesis were distributed to developing grains and, for the most part, not lost in

respiration. Stem dry weight decreases during grain filling have been positively correlated with NSC remobilization to the grain (Rawson and Evans, 1971; Austin et al., 1977).

Wheat stems act as temporary storage organs for NSCs to correct a 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 Clarke, 1982; Frederick and Bauer, 1999). In the absence of stress, the amount of storage appears to be unrelated to yield (Asana and Basu, 1963; Rawson and Evans 1971; Hossain et al., 1990; Borrel et al., 1993). There is good evidence, however, that suggests that temporary NSC storage is very important under stress conditions (Bidinger et al., 1977; Aggrawal and Sinha, 1984). Slafer et al. (1994b) reported that pre-anthesis shading greatly reduced the number of grains from about 15,000 m^{-2} to less than 7,000 m^{-2} through reductions in both number of spikes m^{-2} and number of grains $spike^{-1}$. Under drought conditions, wheat yields may be more dependent on total photosynthate accumulation than photosynthesis during grain fill, since photosynthesis is much more sensitive to low water status than the phloem conducting system which remains functional (Wardlaw, 1967; Slayter, 1969; Hsiao, 1973). In plants with determinate growth habit, essentially all vegetative growth is completed at flowering. As seeds enlarge, not only is current photosynthate partitioned into productive parts, but also, depending on circumstances, stored materials are remobilized (Hendrix, 1995). The early studies of Archbold (1942) on barley

(*Hordeum vulgare* L.), however, cast some doubt on the importance of stem reserves as a source of grain carbon.

The accumulation of carbohydrate reserves appears to confer an evolutionary advantage, serving as a source of carbohydrate to maintain grain filling during periods of drought stress (Gallagher et al., 1976; Kiniry, 1993). Total stem NSCs at anthesis were shown to vary from 50 to 350 g kg^{-1} dry mass in different experiments (Asana and Basu, 1963; McCaig and Clarke, 1982; Davison and Chevalier, 1992; Kiniry, 1993). Gallagher et al. (1976) studied grain growth patterns of field grown winter wheat under drought stressed and nonstressed conditions. In their study, the fraction of final grain weight derived from translocation of materials assimilated before anthesis was greater when conditions during grain filling were adverse for photosynthesis.

Other reports have addressed the relative NSC contribution to grain filling under conditions adverse to current photosynthesis. Austin et al. (1977), using barley crosses between single dwarf parents containing different, nonallelic dwarfing genes, found that the contribution of pre-anthesis assimilates differed between two years studied, 44% in a very hot, dry year but only 11% in a wetter, cooler year. In their experiment, differences among genotypes in the relative NSC contribution to grain filling were not attributable to differences in plant height. Similar findings relative to the influence of plant height were reported by Rawson and Evans (1971). However, Pheloung and Siddique (1991) reported that under dry conditions a modern, semidwarf cultivar utilized more stem NSCs than a modern, tall cultivar. Various authors have studied the effects of dwarfing

genes in wheat (Fischer and Stockman, 1986; Slafer and Andrade, 1993; Miralles and Slafer, 1995), and concluded that dwarfing genes increased the weight of spike tissue at anthesis as a proportion of the total above ground weight.

Aggarwal and Sinha (1984) reported that a drought tolerant cultivar mobilized greater NSCs than a drought susceptible cultivar and that contribution of NSCs was greater for both cultivars under non-irrigated than under irrigated conditions. Pheloung and Siddique (1991) also reported that the NSC contribution to grain filling was greater under non-irrigated conditions than under irrigated conditions.

Postanthesis Water Stress

In wheat, the more severe the water stress at any development stage, or the later in development a stress is applied, the greater the loss of photosynthetic area which is the major carbohydrate source at grain filling (Fischer, 1973). In winter wheat, grain yield is determined by final grain weight, which is dependent on grain filling, and by the number of kernels per unit area, or sink size (Gallagher et al., 1975a; Shanahan et al., 1984). Variability in the number of grains set per ear between wheat cultivars results in a more extensive difference in growth rate per ear than growth rate per grain (Sofield et al., 1977). Modern cultivars possess heavier spikes at anthesis than older cultivars due to their improved capacity for partitioning dry matter during the pre-anthesis period of reproductive development (Slafer et al., 1994b).

The rapid terminal senescence of determinate plants such as the cereals can be assigned, at least in part, to the mobilization of carbohydrate reserves into the developing grain. This pattern of mobilization is accentuated by stress. If for some reason the photosynthetic source remains active during grain filling, the export stem reserves are reduced (Blum, 1988). Almost all the crop dry weight increase in wheat and barley after anthesis can be attributed to grain fill (Slayter, 1969; Gallagher et al., 1975b).

Diverse environmental factors affect both the rate and duration of grain growth in wheat. Assimilate storage does not influence the duration of grain growth (Gallagher et al., 1976). Grain growth rates were increased by more spikelets or grains per spike (Rawson et al., 1983) and decreased by low light levels (Sofield et al., 1977). By far the most important factor influencing grain growth is a dry and hot environment, causing a reduction in the duration of linear growth (Gallagher et al., 1976; Sofield et al., 1977); the rate and duration grain growth may be compensatory if these climatic parameters are not extreme (Gallagher et al., 1976).

Cultivars with high kernel weight under normal water status may experience greater kernel weight reductions under water stress. Cultivars with high kernel weights are often those with fewer kernels per spike (Blum et al., 1983b), low numbers of spikes per unit area (Shanahan et al., 1984), and early anthesis dates (Blum et al., 1983a). In many cases, if total dry matter production exceeds grain fill requirements, as is often the case in nonstress environments,

stem weight rather than grain weight will increase (Slayter, 1969; Gallagher et al., 1975b).

Examination of excised wheat grains has shown that because of increased exposure of cells to diffusional influx of sugars through expanded free endosperm space, sucrose concentrations rise with advancing grain age and eventually decline with maturity (Jenner and Rathjen, 1975). These findings suggest that grain filling duration may not be limited by assimilate availability during grain filling under nonstressed conditions (Jenner and Rathjen, 1975; Rawson and Evans, 1971; Sofield et al., 1977). Since about 70 % of the dry weight of wheat grain is starch, the cessation of starch accumulation and hence grain growth may be limited by the inhibited enzymatic conversion of sugars to starch in developing wheat grains (Jenner and Rathjen, 1975). High air temperatures under water stress may also prematurely affect those changes (Gallagher et al., 1976).

In greenhouse studies, Barlow et al. (1980) showed that with moderate water stress applied to the wheat plant 10 d after anthesis, the water potential of flag leaves, rachis, and glumes dropped after 4 d with grain water potential remaining constant. This resistance to water and osmotic potential changed when other tissues were affected and may be attributed to anatomical and morphological barriers to water loss from wheat grains. These include the lemma, palea, and glumes, partially discontinued by thick walled cells of the xylem tissue to grain, and stress induced lipid deposition in the chalaza zone, which separates the grain from surrounding tissues (Barlow et al., 1980). Since

reduced photosynthesis was caused by sink size reduction (Rawson et al., 1983; Slayter, 1969), and because dryland wheat crops may produce more assimilate than can be used by the grain (Shanahan et al., 1984), it has been suggested that yield may be sink-limited.

At 14 d postanthesis, wheat spikes appear to be the major sink for photo-assimilates (Rawson and Evans, 1971). At this time, 78 to 82 % of the CO_2 requirement is needed for dry weight increase, the rest accounting for dark and photorespiration losses (Evan and Rawson, 1970). The sources of the assimilate are carbohydrates produced and stored before anthesis and postanthesis (current) photosynthesis (Gallagher et al., 1975b; Gallagher et al., 1976). The relative contribution of these sources is determined by photosynthetic area, the active life span of photosynthetic area at spike emergence, and the active life span and the efficiency of photosynthetic tissue after spike emergence (Fischer, 1973). Once final grain number per spike has been determined, these two sources must supply sufficient carbohydrates if maximum grain weight is to be achieved (Gallagher et al., 1975b). Under non-water stressed conditions, post anthesis spike and leaf photosynthesis, which peak during rapid grain growth (Rawson and Evans, 1971), meet and often surpass the demands of grain during the linear phase of grain growth in most cultivars. Exceptions were one awnless type (Evans and Rawson, 1970) and another exhibiting extremely rapid grain growth, both of which required alternate assimilate sources (Rawson and Evans, 1971). The availability of stored assimilate that can be remobilized for grain filling may act as a buffer to grain yield loss under sub-optimal growth conditions, such

as occurs under postanthesis drought (Gallagher et al., 1975b, 1976; Bidinger et al., 1977).

Under drought stress, grain yield is lowered because wilting leaves retain up to 50 % more photosynthate during rapid grain fill (Wardlaw, 1967; Slayter, 1969; McCaig and Clarke, 1982), perhaps due to reduced cell permeability, which subsequently reduces photosynthesis further (Wardlaw, 1967). However, drought stress does not affect the rate of photosynthesis in green tissue (Fischer, 1973). There is little subsequent compensation for postanthesis reduction in photosynthesis since grain growth is a rapid process and almost all plant weight increase thereafter is due to grain fill (Slayter, 1969).

The flag leaf is more photosynthetically efficient than the rest of the canopy during grain fill, partially because it receives the most light (Rawson et al., 1983). Flag leaves of growth chamber-grown wheat senesced over a much longer time course than other leaves (Shanahan et al., 1984), and remained functional one week after grain growth even under high temperatures, as long as water supply was ample (Sofield et al., 1977). Wheat plants water stressed 0 to 14 d postanthesis showed no effect on grain growth when all but the flag were wilted (Asana and Basu, 1963). By 56 d after anthesis, flag leaves of non-water stressed wheat had exported 60% of their photosynthate to the two internodes of the stem and 13% directly to the spike (Wardlaw and Porter, 1967).

Studies of reserve mobilization should take into account the length of time between cessation of stem height increase and the beginning of rapid grain

growth, which greatly affects the amount of reserves available (Rawson and Evans, 1971; Hunt, 1978). Similarly, the period between anthesis and the onset of stem weight reduction is important and variable among cultivar and locations (Rawson and Evans, 1971; Hunt, 1978, Blum et al., 1983a). Cultivars that can draw on stored reserves can stabilize grain dry weight by compensating for a lack of current photosynthesis during grain fill due to drought, high temperatures, disease, or low light conditions (Gallagher et al., 1975b).

Photosynthesis and respiration by wheat spikes, which are largely self-supporting at anthesis, vary among cultivars due to diverse grain and spikelet number and presence or absence of awns, which can increase photosynthesis by 50% (Rawson and Evans, 1971). Spike photosynthesis, which reaches a maximum at much lower light intensity than leaf photosynthesis, provided 20 to 33 % of photosynthesis needed during the linear grain growth phase in awned wheat, depending on cultivar observed, declining rapidly near the end of that phase as the spike matures (Evans and Rawson, 1970). Reduction of spike photosynthesis by shading or drought may decrease yield (Rawson and Evans, 1971; Slayter, 1969), but a compensating increase in flag leaf photosynthesis may minimize the loss (Rawson and Evans, 1971; Evans and Rawson, 1970).

Pre-anthesis drought stress results in reduced kernel number and thus reduced demand for translocation of stored assimilates for supplementation of photosynthesis to meet sink demands during grain fill (Gallagher et al., 1975b). Postanthesis drought stress decreases carbohydrate source size by reducing photosynthetic area (Fischer, 1973). The carbohydrate source size is related to

photosynthesis and yield, rate of flag leaf aging, and the total lifetime CO_2 fixed by the flag leaf (Rawson et al., 1983). In assessing the severity of drought stress on wheat yield, the developmental stage at which it occurs and the sensitivity of that stage must be taken into account (Hsiao, 1973; Slayter, 1969). Maximum yield is achieved only when total crop dry weight is high, and stem weight is low (Gallagher et al., 1975b), which occur if high water status is maintained throughout the crop life cycle (Rawson and Evans, 1971).

Yield Components

Plants of small grain cereal crops progress through a series of well defined developmental stages from germination and establishment, through tiller production, stem extension, and spike emergence to grain filling and maturity (Hay and Walker, 1989, p. 159). While each of these stages is important, improving grain yield is usually the most important objective in plant breeding. However, this has been difficult because of the great number of genes involved and the low heritability of yield itself (Kronstad and Moss, 1989).

Yield components are being formed at any time during the life cycle of the crop, but undoubtedly some phases are more important in determining yield potential than others (Miralles and Slafer, 1999). Several studies have concluded that the period between terminal spikelet initiation and anthesis is of paramount importance (Fischer, 1984; Kirby, 1988; and Perry and D'Antuono, 1989; Slafer et al., 1990). Adams (1967) reported that yield components in common bean (*Phaseolus vulgaris* L.), are interdependent in their development and hence can compensate for each other; thus increasing one yield component will not

necessarily increase the total yield. These relationships are affected under stress and the components most affected by stress conditions are compensated for by other components in the developmental sequence. Johnson et al. (1966) suggested that increases in yield levels are progressively more difficult to obtain and that evaluation of individual yield components might provide a better basis for progeny evaluation than yield itself.

The increase in grain number per unit area has been far more important than changes in the other components (Feil, 1992; Loss and Siddique, 1994; Slafer et al., 1994b). Modern cultivars attain higher grain yields mainly because they are able to set higher number grains per unit area (Calderini et al., 1999). Number of ears per unit area is strongly dependent upon the established plant population density and upon the environmental conditions around the time of terminal spikelet, which determine the proportion of the tillers, which will survive to bear spikes (Hay and Walker, 1989).

Kernel weight is a primary yield component, highly dependent on the rate and duration of grain filling. High temperatures shorten the duration of grain filling unless offset by an increase in the rate of grain filling (Sofield et al., 1977). Bruckner and Frohberg (1987) evaluated 20 diverse spring wheat genotypes in four North Dakota environments. They found that genotypes varied for both grain filling rate and duration and kernel weight was associated with the rate but not the duration of grain filling.

Increased plant population density is often associated with decreased fertile tillers per plant. In a given crop stand, tiller spikes tend to be smaller than main stem spikes, and therefore it might be predicted that the number of grains per spike would increase with increasing density. However, the converse is generally true so that there are opposing trends in the number and size of spikes with changes in plant population density. In general, any variation in management or environment can affect final spike size (Hay and Walker, 1989).

Ledent and Moss (1979) ranked 37 morpho-physiological traits according to the absolute value of their simple correlation coefficient with grain yield per shoot. In all cases, kernel number ranked first in its closeness of association due to the fact that their experimental genotypes tended to produce uniform size kernels on individual spikes. Yield compensation by individual tillers of these cultivars was accomplished primarily by adjustments in kernel numbers and not size.

In addition to improved management, in most wheat growing areas wheat grain yield increases can be attributed to changes in biological yield (i.e., above ground dry matter), harvest index (ratio of grain yield to total or above-ground biomass), or both (Slafer et al., 1994a). Most workers who have studied the physiological basis of genetic improvements in wheat grain yield have concluded that total aboveground biomass at maturity has not substantially changed over the last century (Austin et al., 1980; Waddington et al., 1986; Siddique et al., 1989; Slafer and Andrade, 1991). Therefore, it can be concluded that biomass improvements have not been responsible for increased grain yield as reported by

several authors. Considering that the grain yield portion of the total dry matter produced by the crop has been genetically improved through breeding, and that biomass has increased only slightly (if at all), most of the changes in grain yield have thus been due to increased harvest index. Slafer and Andrade (1991) found a strong parallelism between genetic gains in both grain yield and harvest index.

Siddique et al. (1989) and Slafer et al. (1990) reported that a genotype's capacity for partitioning assimilates between reproductive and vegetative structures (i.e., harvest index) were already evident at anthesis. Modern cultivars possess heavier spikes at anthesis than older cultivars due to the improved capacity of the former for partitioning dry matter during the pre-anthesis period of reproductive development (Slafer et al., 1994b). A reduction in stem and leaf sheath dry matter to 50 % of the current average values, and reallocation of this dry matter to the spike, could raise the harvest index from about 0.5 to 0.62, assuming constant biomass production (Austin et al., 1980). Such a dramatic change may not be possible, or even desirable, in view of the stems' role in supporting the spike and maintaining an effective display of leaves for light interception. Therefore, increases in total dry matter may provide the most likely route to further increase in yield (Waddington et al., 1986).

Chemical Desiccation

Boyer and McPherson (1975) stated that under severe postanthesis drought stress, plant reserve mobilization might represent an important factor for stress tolerance, especially when the tolerance of the translocation process to water deficit is considered. The identification en masse of such tolerant genetic

materials by using ambient stress environments is difficult and time consuming, due to their inherently erratic and unpredictable nature. A controlled method is required to identify genotypes that can sustain translocation-based kernel growth in presence of reduced current photosynthesis (Blum et al., 1983a; Blum, 1998).

Blum et al. (1983a) proposed the use of a contact chemical desiccant as a screen for genetic materials that can support grain growth from stored stem NSCs in the absence of photosynthesis. Magnesium chlorate ($MgClO_4$) was applied to wheat canopies 14 d postanthesis, inducing complete elimination of the current photosynthetic source within 48 hours. Stem and kernel measurements during grain filling showed a reduction in both rate and duration of grain filling and that greater stem dry weight losses following desiccation were associated with compensatory increases in kernel growth rate and reductions in kernel weight injury in response to the chemical desiccant. In a companion study, Blum et al. (1983b) found that kernel weight injury by chemical desiccation was significantly and positively associated with kernel weight injury by late-season drought stress in the field.

Hossain et al. (1990) used chemical desiccation (with sodium chlorate, $NaClO_3$) on hard red winter wheat genotypes varying in stress tolerance and yield potential. They reported that grain yield and kernel weight in dryland plots were positively associated with grain yield and kernel weight under chemical desiccation. However, both grain yield and kernel weight in well-watered plots were not strongly correlated with desiccation injury for grain yield and kernel weight in chemically desiccated plots. Stem sampling indicated that desiccated

plants retained more NSCs in their stem parts than did plants of control plots and that dry matter and NSC losses from the stems of desiccated plants were not strongly correlated with yield and kernel weight injury. Their conclusions regarding chemical desiccation were more based more on the cultivar performance records than results correlated with stem NSCs analyses.

Turner and Nicolas (1987), Turner et al. (1989) and Nicolas and Turner (1993) compared several desiccants and senescing agents. All chemicals evaluated were found to induce uneven desiccation or senescence of spikes and large reductions in kernel weight when applied to whole plants (spikes included). However, when only leaves and stems were sprayed, potassium iodide (without any direct toxic effects on grain filling) had comparable effects on grain growth to manual defoliation and was judged to be the best chemical for field use. They concluded that potassium iodide treatment showed promise as a selection technique to identify wheat lines maintaining stable kernel weight during drought through high contribution of stem reserves, spike photosynthesis, or both.

Haley and Quick (1998) compared wheat cultivar responses to different chemical desiccants and dates of desiccant application and examined grain filling and stem dry weight loss patterns to assess the suitability of chemical desiccation as a screening method for postanthesis drought stress tolerance. In their study they found that chemical desiccation resulted in apparent reduction in grain filling rates and increased stem dry weight losses during grain filling. Also, cultivars that were tolerant of chemical desiccation demonstrated increased stem

dry weight immediately after anthesis and subsequent increased rates and amounts of stem dry weight loss during grain filling.

Relatively few breeding and genetic studies with chemical desiccation have been reported in the literature. Mahalakshmi et al. (1994) used potassium iodide to evaluate hybrid pearl millets (*Pennisetum glaucum* L.) for genetic response to water deficit during grain filling. Haley and Quick (1998) used $NaClO_3$ effectively in early generations to identify bulk populations tolerant of chemical desiccation.

CHEMICAL DESICCATION INJURY AND DRYLAND PERFORMANCE OF WINTER WHEAT

Abstract

Winter wheat (*Triticum aestivum* L.) often experiences postanthesis drought stress that causes crop yield and quality losses. Contact chemical desiccants have been proposed as a means to identify genotypes with improved ability to support grain filling from stem nonstructural carbohydrates (NSC) in the absence of photosynthesis during grain filling. The objectives of this study were to characterize chemical desiccation response and dryland performance of F_2 derived lines and their parents, determine associations between chemical desiccation injury and dryland performance, and estimate genotypic variance components of traits measured under chemical desiccation. $F_{2:4}$ lines from six crosses with seven parents were planted in a split-plot with two replications in 1998 and 1999 under irrigation at Fort Collins, CO. Sodium chlorate ($NaClO_3$, 2% W:V, 125 mL m^{-2}) was applied to subplots 15 d postanthesis. The same lines were also evaluated at four dryland locations (Akron in 1998 and Burlington, Akron, and Walsh in 1999) in a randomized complete block design with two replicates. Yield injury from chemical desiccation ranged from 13 to 37% among entries, with reductions in both kernel weight (13 to 23%) and kernel number (8 to 32%). Significant associations were observed between grain yield injury and both biomass injury ($r=0.65$, $P<0.05$) and kernel weight ($r=0.57$, $P<0.05$).

Average performance under dryland conditions was less than that observed under chemical desiccation, although test weight was much less under desiccation than under dryland conditions. Grain yield under dryland conditions was not associated with either grain yield injury or kernel weight injury under chemical desiccation. Significant genotypic variance for most traits examined was observed, suggesting that progress in selection may be realized within these populations. Inconsistency in entry desiccation tolerance, and the lack of correlation between desiccation tolerance and dryland performance, suggest that additional research is necessary to identify strategies and techniques to successfully exploit the chemical desiccation method in applied wheat breeding programs.

Introduction

Drought stress, often in combination with high temperature stress, is one of the most important constraints to wheat production in many wheat growing regions (Slafer and Andrade, 1993; Slafer et al., 1994; Simmons, 1987). Drought stress during the grain filling period (postanthesis) affects availability and translocation of photosynthates to the developing kernel, resulting in reduced weight and grain quality (Hawker and Jenner, 1993). Wheat breeders and physiologists have attempted to identify specific traits that enhance wheat adaptation and increase or stabilize grain yield in drought prone areas.

Wheat grain growth is dependent on gross photosynthetic rate, stored nonstructural carbohydrates (NSC) in the stem at anthesis, initial kernel dry weight, and the maximum rate and duration of kernel growth (Blum, 1998). When

photosynthetic performance of the plant is inhibited by postanthesis drought stress, kernel growth becomes increasingly dependent on NSC stored prior to and at anthesis (Austin et al., 1980). Under such conditions, sustained kernel growth with limited transient photosynthesis is extremely important to mitigate the adverse effects of drought stress (Blum, 1998). Stem NSC reserve mobilization is a major tolerance factor, especially when the tolerance of the translocation process to water deficit (relative to synthesis) is considered (Boyer and McPherson, 1975).

The use of field environments for empirical selection for postanthesis drought stress tolerance may be impractical due to their inherently erratic nature and the complicating effects of variability in plant phenology. Blum et al. (1983a,b) and Blum (1998) proposed the use of a contact chemical desiccant ($MgClO_4$) as a means of separating genotypes based on the ability to support grain filling from stem NSC 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. Blum et al. (1983a) reported a negative association between kernel weight injury by chemical desiccation and kernel weight under drought stress. Desiccation treatment does not simulate drought stress *per se*; rather it simulates a direct effect of stress by inhibiting current assimilate production (Blum, 1998). Hossian et al. (1990) reported positive associations between grain yield and kernel weight under dryland and chemically desiccated ($NaClO_3$) conditions. Nicolas and Turner (1993) and Haley and Quick

(1993, 1998) indicated that the chemical desiccation method was useful for selection of potential parents and advanced lines and was effective in early generations for identifying crosses that are tolerant of chemical desiccation. In other crops, chemical desiccation as a means for identifying variation in grain filling from stem NSC has been evaluated in pearl millet (*Pennisetum glaucum* L.; Mahalakshmi et al., 1994) and sorghum (*Sorghum bicolor* L.; Blum, 1998).

Information on genetic parameters for chemical desiccation response of lines derived from crosses between contrasting parents is lacking. Comstock and Moll (1963) pointed out that genetic effects are functions of the specific environment population with respect to which they are defined. Furthermore, the genetic effect that has meaning for the plant breeder invariably pertains to an environment and population that has dimensions in both time and space. To obtain unbiased estimates of genetic variance, an appropriate complex of genetic families must be evaluated in more than one location and year. However, estimates of variance estimates across populations and environments provide an overall indication of amount of each type of genetic variance (Bernardo, 2002). The objectives of this study were to:

a) characterize chemical desiccation response of F_2-derived winter wheat lines and their parents under irrigation and under dryland conditions;
b) determine the association between chemical desiccation injury under irrigation and dryland field performance among the F_2-derived wheat lines and parents; and

c) estimate genotype, genotype x environment, and error variance components for chemical desiccation response among F_2-derived wheat lines.

Materials and Methods

Line derivation

In 1994, crosses were made in the greenhouse among seven hard red winter and hard white winter wheat genotypes including, 'Arlin', 'Rio Blanco', 'Vista', 'Lamar', 'KS85W663-11-1', 'KS85W663-11-8', and 'KS87W822-2-1'. Lamar, Vista, and Rio Blanco are wheat cultivars with good adaptation for dryland production in the west-central Great Plains while Arlin, KS85W663-11-8, KS85W663-11-1 and KS87W822-2-1 are genotypes that have shown drought stress symptoms under dryland conditions in eastern Colorado (Dr. J.S. Quick, personal communication).

In 1995-1996, F_2 populations from the six crosses, Arlin/Lamar, Rio Blanco/Lamar, Rio Blanco/Vista, KS85W663-11-8/Lamar, KS85W663-11-1/Lamar, and KS87W822-2-1/Lamar were space planted in a field nursery. In 1996-1997, $F_{2:3}$ rows were grown in the field and rows with good visual appearance were harvested in bulk. Two hundred and eighty eight $F_{2:4}$ derived lines (48 lines per population) were grown in the field study in 1997-1998 along with the seven parents. Sixty eight $F_{2:4}$ lines (four to eighteen lines per population), chosen to represent a broad range of performance characteristics in 1998, were grown in the field study in 1998-1999.

Year 1 (1997-1998)

Field experiments were conducted during 1997-1998 (1998) at Fort Collins (irrigated) and Akron (dryland). The Fort Collins location was planted on 27 September 1997 at the Colorado State University Agricultural Research Development and Education Center (ARDEC). Field plots were planted in two rows 3.4 m long on raised beds 0.76 m apart with two rows 20 cm apart on each bed (effective experimental unit area 5.2 m^2). The average seeding rate was 50 kg ha^{-1}. Entries (derived lines and parents) were planted in a split plot arrangement in a randomized complete block design with two replicates. Entries were considered as main plots and treatments (control and chemical desiccant) as subplots. Sodium chlorate ($NaClO_3$, 2% W:V, 125 mL m^{-2}) was applied to plots 15 days postanthesis with a CO_2-propelled backpack spray apparatus.

The Akron location was planted on 19 September 1997 in a randomized complete block design with two replications. Field plots were six rows, 3.7 m long 0.3 m apart. Only the center four rows were used for grain yield and test weight analysis (effective experimental unit area 4.4 m^2). The average seeding rate was 42 kg ha^{-1}.

At Fort Collins, the number of days from January 1 to anthesis was recorded when about 50% of the spikes in a plot showed anthers in the central one-third of the spike. Plots at both locations were machine harvested at maturity for grain yield estimates. For yield component analysis, small sections from each plot (0.5 m long at Fort Collins, 1 m long at Akron) were hand-harvested at harvest maturity. Kernel weight was estimated from a random sample of six

spikes from the hand-harvested sample. Kernel number, biomass, and grain yield were estimated from the hand-harvested sample. Test weight was estimated from a sample about 250 g of the combine-harvested grain. Harvest index was estimated from the ratio of grain weight and biomass in the hand-harvested sample.

Year 2 (1998-1999)

In the 1998-1999 season (1999), field experiments were conducted under irrigation at Fort Collins and under dryland conditions at Akron, Burlington and Walsh, CO. The Fort Collins location was planted on 28 September 1998. Dryland experiments were planted 23 September at Akron, 16 September at Burlington, and 23 September 1998 at Walsh. All other experimental details [e.g., plot dimensions, experimental design, seeding rate, desiccant application (Fort Collins only), and data collection] were done as in 1998.

Data analysis

Proc GLM in SAS was used for analysis of variance (ANOVA). A combined ANOVA across environments was done after testing error mean square for homogeneity according to Bartlett's test (Gomez and Gomez, 1984). Environments and entry were considered as random effects. Data were averaged across lines from the same cross to create a single replicate value for each population of lines. Percent desiccation injury was calculated for grain yield, test weight, kernel weight, kernel number, biomass, and harvest index according to the following formula:

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

Fischer's protected Least Significant Difference (LSD) was used to compare genotype and treatment means for all measured variables. Simple Pearson correlations coefficients between means for all measured were calculated using the Proc CORR procedure of SAS.

For traits measured at Fort Collins, components of variance among lines within a family were estimated from the ANOVA as described in Fehr (1987) and Hallauer and Miranda Filho (1988). Environments (years) and genotypes were both considered as random effects in the model. Each population was analyzed independently. The genotypic variance component (σ^2_g) was estimated assuming that the variance among inbred lines is equal to the expected mean squares for the genotype x environment (year) interaction minus the expected mean square for genotypes divided by the number of years and number of replications (Hallauer and Miranda Filho, 1988):

$$\sigma_g^2 = \frac{(MS_g - MS_{gxe})}{ry}$$

where MS_g is the mean square among genotypes, MS_{gxe} is the mean square of genotype x environment interaction, r is the number of replications within each location; and y is the number of years. Similarly, the variance for the genotype x environment interaction was calculated as:

$$\sigma^2_{gxe} = \frac{(MS_{gxe} - MS_{error})}{r}$$

The size of the variance component for each trait is dependent on the units of measure for the trait. Therefore, it is necessary to standardize the

variance components as a fraction of the total or non-environmental variation (year and replication in this experiment) prior to direct comparison of variances (Basset et al., 1989; Graybosch et al., 1996). Genotypic variance was standardized as a percent of the total non-environmental variation using the formula:

$$\text{Standardized } \sigma_g^2 = \frac{\sigma_g^2}{[(\sigma_g^2 + \frac{\sigma_{gxe}^2}{y}) + (\frac{\sigma_{error}^2}{ry})]}$$

The standard errors for the standardized variance among genotypes were estimated from the ANOVA as:

$$SE\ \sigma_g^2 = \sqrt{\frac{2}{(re)^2} x (\frac{M_4^2}{n+1} + \frac{M_3^2}{(e-1)(n-1)+2})}$$

where r is the number of replications within an environment, e is the number of environments, M_3 is the genotype x environment interaction mean square, and M_4 is the genotype mean square (Hallauer and Miranda Filho, 1988).

Results and Discussion

Climatic conditions

Precipitation and rainfall data during the growing season for the six environments are shown in Table 1. Total precipitation in 1998 at Akron was 43% below the long-term average while total precipitation in 1999 was the same as the long-term average. Maximum temperature was similar for both growing seasons. The maximum temperature at Fort Collins was near the long-term average. In 1999, total precipitation was 34% higher than the long-term average

at Burlington and near the long-term average at Walsh. Maximum temperatures were near the long-term average at these sites. Among the dryland locations, precipitation during the growing season was the greatest at Burlington in 1999 (372 mm), followed by Walsh 1999 (311 mm), Akron 1999 (275 mm), and Akron 1998 (155 mm). In 1999, Burlington was damaged by a hailstorm prior to harvest and there was some grain and biomass loss and lodging damage.

Irrigated trait evaluation (control and desiccated treatments)

Highly significant differences were observed for most sources of variation for most traits analyzed. Environment x entry, environment x treatment, entry x treatment, and environment x entry x treatment interaction effects for grain yield and yield components were significant, indicating variability of entry and environmental response to chemical desiccation.

Values for traits measured under the control and desiccated treatments and chemical desiccation injury are shown in Tables 2 and 3. Significant differences among entries were observed for grain yield, test weight, kernel weight, kernel number, biomass and harvest index. The range of chemical desiccation injury among derived lines was less than their parents for all variables examined. Grain yield of entries ranged from 4341 to 5412 kg ha^{-1} under the control treatment and 3222 to 4300 kg ha^{-1} under chemical desiccation. Yield injury from chemical desiccation ranged from 13 to 37%.

Table 1. Precipitation and maximum air temperature during the growing season at Fort Collins, Akron, Burlington and Walsh in 1998 and 1999.

	1998	1999			1998		1999			
Month	Akron	Akron	Burlington	Walsh	Fort Collins	Akron	Fort Collins	Akron	Burlington	Walsh
	precipitation (mm)				maximum air temperature (^{0}C)					
March	3.8	7.1 (24.6)†	13.2 (25.7)	46.0 (23.4)	10.8	9.5	14.7 (11.9)	13.9 (10.9)	13.8 (12.2)	12.7 (14.4)
April	19.6	57.4 (32.0)	109.2 (30.2)	94.7 (39.6)	15.7	15.6	13.6 (16.4)	14.1 (15.8)	14.9 (17.4)	18.5 (19.3)
May	25.2	54.9 (77.5)	84.6 (75.7)	107.2 (70.4)	23.2	24.7	20.3 (26.7)	21.2 (20.9)	22.0 (22.4)	23.3 (24.3)
June	9.1	87.4 (63.0)	95.3 (67.1)	14.2 (67.3)	24.7	26.8	25.7 (26.7)	26.9 (27.3)	27.6 (28.7)	29.7 (30.4)
July	97.5	68.6 (73.9)	69.3 (78.7)	48.5 (95.0)	30.2	31.6	30.3 (29.7)	32.4 (31.6)	34.0 (31.9)	33.8 (33.3)
Total	155.2	275.4 (271.0)	371.6 (250.4)	310.6 (295.7)						

† Twenty year average data are in parentheses.

There was generally very little difference in desiccation injury or yield between derived-lines and their parents under desiccation. Derived lines (5037 kg ha^{-1}), however, showed greater yield than the parents (4984 $kgha^{-1}$) under the control treatment. Entries considered as more sensitive to drought stress, such as KS85W663-11-1 and KS87W822-2-1, were remarkably tolerant of the chemical desiccation and showed relatively less desiccation injury than Lamar (Table 2). Significant differences among entries were observed for test weight under both the control and desiccated treatment and for chemical desiccation injury (Table 2). The difference in test weight between the control and desiccated treatments was generally small, approximately 6% lower in the desiccated treatment relative to the control. The dryland-adapted cultivar Lamar showed the highest test weight under both control and desiccated treatments and the lowest test weight injury among the entries tested. For the drought stress-sensitive experimental line KS85W663-11-1, low test weight under both control and desiccated conditions and high test weight injury were observed. Genotypes with low test weight might have been more sensitive to the desiccation treatment, which inhibits grain filling and increases the degree of grain shriveling (Schuler et al., 1994). Significant differences among entries were observed for both kernel weight (Table 2) and kernel number under (Table 3) the control and desiccation treatments and in terms of chemical desiccation injury. Desiccation injury ranged from 13 to 23% for kernel weight and from 8 to 32% for kernel number.

Table 2. Grain yield, test weight, and kernel weight for parents and derived lines averaged over two years of evaluation under irrigated and desiccated conditions at Fort Collins, 1998 and 1999.

Genotype	Grain yield			Test weight			Kernel weight		
	control	desiccated	injury[†]	control	desiccated	injury	control	desiccated	injury
	----kg ha^{-1} -----		---%---	— kg m^{-3} ———		--% ---	------mg kernel^{-1}——		--%---
Parent									
Arlin	5173	3222	37	768	738	4	39.0	30.0	23
Lamar	5207	3809	26	777	757	3	36.8	30.8	16
Rio Blanco	4341	3302	23	764	706	8	29.3	24.3	17
Vista	5412	3784	29	758	702	8	35.8	30.0	16
KS85W663-11-8	5376	4300	20	769	721	7	33.0	27.5	17
KS85W663-11-1	4647	3994	13	760	689	10	34.5	30.0	19
KS87W822-2-1	4738	3984	16	757	723	5	33.0	27.0	13
Derived line group									
Arlin/Lamar	5161	3792	26	774	726	6	37.9	29.3	20
Rio Blanco/Lamar	5126	3791	25	769	723	7	35.2	27.8	21
Rio Blanco/Vista	4959	3619	26	756	711	6	34.7	27.5	18
KS85W663-11-8/Lamar	5220	3673	27	764	718	7	36.3	29.8	15
KS85W663-11-1/Lamar	4807	3907	18	763	735	5	35.6	31.6	13
KS87W822-2-1/Lamar	4949	3812	20	767	731	5	34.4	29.2	14
Mean	5009	3769	24	765	722	6	35.0	28.8	17
CV (%)									
Entry	4		10	2		42	4		21
Treatment	5			3			5		
LSD (0.05)									
Entry	189		4	17		4	1.2		5
Treatment	41			5			0.4		

[†]Calculated as % injury = [(control-desiccated)/control]*100.

Table 3. Kernel number, biomass, and harvest index for parents and derived lines averaged over two years of evaluation under control and desiccated conditions at Fort Collins, 1998 and 1999.

Genotype	Kernel number			Biomass			Harvest index		
	control	desiccated	injury[†]	control	desiccated	injury	control	desiccated	injury
Parent	-----kernels m^{-2}-----		--%--	--------- g m^{-2} --------		--% --			--%--
Arlin	816	570	31	2110	1613	24	0.30	0.24	20
Lamar	965	782	17	2784	2276	18	0.29	0.27	8
Rio Blanco	1231	998	19	2257	1794	20	0.37	0.28	26
Vista	1130	941	17	2157	1618	25	0.30	0.27	16
KS85W663-11-8	1081	780	32	2321	1937	17	0.28	0.23	13
KS85W663-11-1	978	899	8	2637	2103	18	0.26	0.24	11
KS87W822-2-1	1094	809	29	2503	2176	13	0.27	0.24	19
Derived Line Group									
Arlin/Lamar	918	793	21	2414	1895	17	0.29	0.24	16
Rio Blanco/Lamar	1000	803	13	2337	1841	15	0.28	0.24	21
Rio Blanco/Vista	1156	905	15	2242	1763	17	0.34	0.24	22
KS85W663-11-8/Lamar	1017	806	21	2611	2045	16	0.27	0.23	13
KS85W663-11-1/Lamar	876	714	15	2350	1946	14	0.28	0.25	17
KS87W822-2-1/Lamar	961	776	17	2601	2035	16	0.25	0.22	20
Mean	1017	814	20	2410	1926	18	0.29	0.25	17
CV (%)									
Entry		8	21		7	36		13	32
Treatment		11			8			11	
LSD (0.05)									
Entry		72	6		161	9		0.04	8
Treatment		15			53			0.01	

[†]Calculated as % injury = [(control –desiccated)/control]*100.

Arlin and the Arlin/Lamar population showed high desiccation injury for kernel weight. In spite of high desiccation injury, Arlin and the Arlin/Lamar population had high kernel weight under the control and desiccation treatments than most other populations. Lamar, Vista, and the KS85W663-11-8/Lamar and KS85W663-11-1/Lamar populations showed lower kernel weight injury and higher kernel weight under both control and desiccated treatments than many of other entries. With regard to kernel number responses to chemical desiccation, Arlin and the Arlin/Lamar population showed significantly lower kernel number under both control and desiccated conditions and higher kernel number injury. Lamar and both the KS85W663-11-1/Lamar and KS87W822-2-1/Lamar populations showed significantly lower level kernel number injury even though they showed significantly lower kernel number under both the control and desiccated treatments. Significant differences among entries were observed for both biomass and harvest index under the control and desiccation treatments and in terms of chemical desiccation injury (Table 3). Desiccation injury ranged from 13 to 25% for biomass and 8 to 26% for harvest index. Some entries that performed well under the control and desiccated treatments showed a high injury response for both biomass and harvest index.

Chemical desiccation injury identified entries that were tolerant, sensitive, and moderate. Entries that were expected to be more tolerant of desiccation (e.g., Lamar and Vista) tended to have higher injury for yield and yield components. Entries that were expected to be more sensitive to chemical

desiccation (e.g., KS85W663-11-1 and KS87W822-1) showed inconsistent levels of injury for most of traits and little apparent trend in chemical desiccation tolerance.

Pearson correlation analyses were conducted to determine if associations exist between grain yield and yield components measured under control and chemical desiccation injury (Table 4). The only correlation observed among desiccation injury variables was a positive correlation between grain yield injury and biomass injury ($r=0.65$, $P<0.01$). A significant association was also observed between grain yield injury and kernel weight in the control treatment ($r = 0.57$, $P<0.05$). Austin (1999) suggested that substantial genetic gain in yield might be achieved with greater biomass at maturity. Blum et al. (1983b) reported that reduced kernel weight under chemical desiccation was strongly associated with non-stressed kernel weight. However, no such correlation was observed in this experiment and in experiments reported by Nicolas and Turner (1993). Furthermore, no correlation was observed in this experiment between grain yield injury and injury for test weight, kernel weight, or kernel number.

Harvest index injury was associated with control biomass ($r=-0.63$, $P<0.05$) and control harvest index ($r=0.56$, $P<0.05$). Correlations were also calculated between other variables measured in the experiment (Table 4). Control grain yield was significantly associated with control kernel weight ($r=0.64$, $P<0.05$) while a negative correlation was observed between kernel weight and kernel number ($r=-0.78$, $P<0.01$). Harvest index was associated with both kernel number ($r=0.57$, $P<0.05$) and biomass ($r=-0.56$, $P<0.05$).

Table 4. Pearson correlation coefficients between variables measured at Fort Collins in 1998 and 1999.

	Grain yield injury[†]	Test weight injury	Kernel weight injury	Kernel number injury	Biomass injury	Harvest index injury	Control grain yield	Control test weight	Control kernel weight	Control Kernel number	Control Biomass
Test weight injury	-0.35										
Kernel weight injury	0.54	0.14									
Kernel number injury	0.30	-0.39	0.04								
Biomass injury	0.65**	0.15	0.46	0.11							
Harvest index injury	0.13	0.11	0.14	0.08	0.04						
Control grain yield	0.53	-0.24	0.19	0.30	0.27	-0.46					
Control test weight	0.29	-0.44	0.31	0.15	-0.01	-0.34	0.36				
Control kernel weight	0.57*	-0.43	0.38	0.04	0.23	-0.41	0.64*	0.37			
Control kernel number	-0.19	0.46	-0.27	-0.05	0.05	0.34	-0.27	-0.49	-0.78**		
Control biomass	-0.48	-0.13	-0.40	-0.30	-0.51	-0.63*	-0.10	0.31	0.03	-0.18	
Control harvest index	0.36	0.09	0.23	0.01	0.39	0.56*	-0.32	-0.15	-0.38	0.57*	-0.56*

*, ** Significant at 0.05 and 0.01 probability levels, respectively. (n=13).

[†] Injury variables calculated as % injury = [(control-desiccated)/control]*100.

Dryland trait evaluation

Experiments were conducted under dryland environments to evaluate the pattern of genotype response and associations between dryland response and chemical desiccation injury (Table 5 and 6). Significant differences were observed among entries for all traits measured under dryland conditions. Parent entries showed a wider range of response than the groups of derived lines for test weight, kernel weight and harvest index except for grain yield biomass and kernel number. The Rio Blanco/Vista, Rio Blanco/Lamar, and Arlin/Lamar populations had higher grain yield values than the other populations and parent entries. Lamar and the Arlin/Lamar and Rio Blanco/Lamar populations had higher test weight values than the other populations and parental entries. Average grain yield over dryland locations (3222 kg ha^{-1}) was less than average grain yield under chemical desiccation at Fort Collins (3769 kg ha^{-1}) and in each case entry grain yield was higher under chemical desiccation than under dryland conditions (Tables 2 and 5). Test weight under dryland conditions (762 kg m^{-3}), however, was higher than that observed under chemical desiccation at Fort Collins (722 kg m^{-3}), suggesting some dissimilarity in grain filling capacity under dryland and chemical desiccation conditions. Under the dryland conditions, Arlin and the Arlin/Lamar and KS85W663-11-1/Lamar populations had numerically higher kernel weight values than other populations and parental entries. These entries also showed an inverse relationship between kernel weight and kernel number as they also had the lowest kernel number among the entries tested (Frederick and Camberatto, 1995; Slafer and Andrade, 1993). No difference in kernel weight

Table 5. Grain yield, test weight, kernel weight, kernel number, biomass, and harvest index for parents and derived lines averaged over four dryland environments (Akron 1998, Akron 1999, Burlington 1999, and Walsh 1999) in 1998 and 1999.

Genotype	Grain Yield	Test Weight	Kernel Weight	Kernel Number	Biomass	Harvest Index
Parent	kg ha^{-1}	kg m^{-3}	mg $kernel^{-1}$	kernels m^{-2}	g m^{-2}	
Arlin	3164	770	32.5	560	1061	0.34
Lamar	3018	778	28.9	667	1165	0.31
Rio Blanco	2980	765	27.4	720	1086	0.38
Vista	3371	743	28.3	760	1076	0.35
KS85W663-11-8	3409	756	28.2	738	1265	0.28
KS85W663-11-1	3298	764	28.7	684	1189	0.28
KS87W822-2-1	2964	752	27.1	656	1196	0.28
Derived Line Group						
Arlin/Lamar	3410	773	30.6	643	1217	0.31
Rio Blanco/Lamar	3414	771	28.6	697	1194	0.30
Rio Blanco/Vista	3585	755	28.7	788	1162	0.33
KS85W663-11-8/Lamar	3055	758	28.2	683	1213	0.28
KS85W663-11-1/Lamar	3324	767	29.7	654	1264	0.29
KS87W822-2-1/Lamar	2891	759	27.8	674	1205	0.28
Mean	3222	762	28.8	686	1176	0.31
CV (%)	12	1	6	15	12	11
LSD (0.05)	375	11	1.8	107	146	0.04

Table 6. Pearson correlation coefficients calculated between variables measured under dryland conditions and under chemical desiccation at Fort Collins in 1998 and 1999.

	Dryland grain yield	Dryland test weight	Dryland kernel weight	Dryland kernel number	Dryland biomass	Dryland harvest index
Grain yield injury	0.11	0.15	0.60*	-0.21	-0.62*	0.57*
Test weight injury	0.31	-0.38	-0.36	0.50	-0.04	0.07
Kernel weight injury	0.43	0.43	0.65*	-0.24	-0.40	0.34
Kernel number injury	-0.21	-0.15	0.19	-0.33	-0.05	0.00
Biomass injury	0.08	-0.14	0.39	0.00	-0.83***	0.71**
Harvest index injury	-0.03	-0.15	-0.07	0.11	-0.37	0.52
Dryland test weight	-0.09					
Dryland kernel weight	0.30	0.51				
Dryland kernel number	0.42	-0.57*	-0.64*			
Dryland biomass	0.16	0.10	-0.21	0.04		
Dryland harvest index	0.06	0.00	0.17	0.18	-0.84***	

* Significant at 0.05, 0.01, and 0.001 probability levels, respectively. (n=13)

was observed between desiccated and dryland treatments. There was, however, higher average kernel number in the desiccated treatment (814 m^{-2}) when compared to dryland conditions (686 m^{-2}). Entries with high above-ground biomass, such as KS85W663-11-8 and the KS85W663-11-1/Lamar, Arlin/Lamar, and KS85W663-11-8/Lamar populations, showed the lowest harvest index. Entries with lower biomass, such as Arlin, Vista, and Rio Blanco also had greater harvest index. This relationship was also evident under desiccation where high biomass (1926 g m^{-2}) and low harvest index (0.29) was observed, compared to the dryland treatment which had relatively low biomass (1176 g m^{-2}) and higher harvest index (0.31).

Pearson correlation coefficients were calculated to assess the association between dryland performance and chemical desiccation injury (Table 6). No significant associations were observed between dryland grain yield, test weight, and kernel number and any of the chemical desiccation injury variables. The lack of association may be due to the relatively low chemical desiccation injury observed and the higher grain yield under desiccation (3769 kg ha^{-1}) compared to the average dryland yield (3222 kg ha^{-1}). Kernel weight under dryland conditions was associated with both grain yield injury ($r=0.60$, $P<0.05$) and kernel weight injury ($r=0.65$, $P<0.05$). This observation suggests that prevailing environmental conditions at the dryland locations were not adverse for grain filling and kernel weight development. Biomass under dryland conditions was negatively associated with both grain yield injury ($r=-0.62$, $P<0.05$) and biomass injury ($r=-0.83$, $P<0.001$) while harvest index under dryland conditions was

positively associated with both grain yield injury ($r=0.57$, $P<0.05$) and biomass injury ($r=0.71$, $P<0.01$).

Correlations among variables measured under dryland conditions likewise revealed few significant associations. Kernel number was negatively associated with both test weight ($r=-0.57$, $P<0.05$) and kernel weight ($r=-0.64$, $P<0.05$) and harvest index was negatively associated with biomass ($r=-0.84$, $P<0.001$).

Genotypic variance estimates

Six different populations were used to examine genetic parameters of traits measured under chemical desiccation in 1998 and 1999 (Table 7). These populations were derived from crosses between divergent parents for drought tolerance and overall dryland adaptation. In 1998, each population consisted of 48 lines while in 1999 population size varied from 4 to 18. In general, higher means for traits were observed in 1999 compared to 1998, with the exception of kernel weight, which was lower in 1999 than 1998. Trait variability among derived lines within a population, however, was greater in 1998 than in 1999 with the exception of kernel number which showed a much narrower range in 1998 than in 1999 due to the low kernel numbers observed. The KS87W822-1/Lamar and KS85W663-11-1/Lamar populations performed better for many of the traits in both years. The KS85W663-11-8/Lamar and KS87W822-1/Lamar populations, both relatively wider crosses from the standpoint of dryland adaptation, had larger ranges than other populations for several traits. The Arlin/Lamar and KS85W663-11-8/Lamar populations had higher grain yield than their parents under both treatments. However, all populations in 1999, except the Rio

Blanco/Lamar population, had higher test weight than the parents under both treatments. Populations had higher kernel weight than the parents under both treatments in 1998 and higher kernel number than the parents under both treatments in 1999. In 1999, all populations had higher biomass than parents in both treatments; however, all populations in both years had lower harvest index than the parents under both treatments (Tables 2, 3, and 7). The populations had ranges for most traits beyond the parental values. It was evident that the populations grown under desiccation had a wide range of variability for means and ranges, especially in 1998.

Means, ranges of five of the six populations, over two years under chemical desiccation are presented in Table 8. Populations were characterized for performance under desiccation to identify the best populations. The Rio Blanco/Lamar population had the highest F-value of genotypes among the populations. The Rio Blanco/Lamar population had the highest F-value of genotypes among the populations for grain yield followed by Rio Blanco/Vista and Arlin/Lamar (Table 8). The population KS87W822-2-1/Lamar had the highest population mean for grain yield and the widest range among the populations.

The Rio Blanco/Lamar population had the highest F-value of genotypes for test weight among the populations followed by the Arlin/Lamar and KS85W663-11-8/Lamar populations. The Arlin/Lamar population had the highest means for test weight. The KS85W663-11-8/Lamar population had the highest F-

Table 7. Mean, minimum, maximum, and significance of F test for genotype effect for grain yield, test weight, kernel weight, kernel number, biomass, and harvest index of six populations grown under chemical desiccation at Fort Collins in 1998 and 1999.

	1998						1999					
Population	Grain Yield	Test weight	Kernel weight	Kernel number	Biomass	Harvest index	Grain yield	Test weight	Kernel weight	Kernel Number	Biomass	Harvest index
	kg ha^{-1}	kg m^{-3}	mg $kernel^{-1}$	kernels m^{-2}	g m^{-2}		kg ha^{-1}	kg m^{-3}	mg $kernel^{-1}$	kernels m^{-2}	g m^{-2}	
Arlin/Lamar (16) †												
Mean	4010	675	32.0	468	1820	0.23	3600	789	28.9	994	2167	0.27
Minimum	3307	664	25.5	315	1273	0.18	2909	766	34.0	690	1807	0.20
Maximum	4644	726	36.5	636	2405	0.37	4240	815	26.0	1226	2636	0.34
F value genotype	6.01***	2.77***	2.42**	4.25***	30.8***	3.69***	5.36**	5.31**	0.95ns	7.85***	0.82ns	1.69ns
Rio Blanco/Lamar (9)												
Mean	4022	664	28.5	616	1896	0.23	3394	769	26.9	1123	2044	0.26
Minimum	3176	553	21.0	395	1302	0.18	2567	712	23.0	910	1645	0.20
Maximum	4813	709	35.5	823	2169	0.39	4158	808	32.0	1265	266	0.31
F value genotype	3.96***	5.74***	3.16***	11.08***	3.76***	3.78***	42.76***	13.44***	2.64ns	4.18*	4.21*	2.69ns
Rio Blanco/ Vista (10)												
Mean	3807	654	29.5	681	1669	0.26	3449	765	27.0	1282	2043	0.27
Minimum	2842	574	24.5	450	1389	0.23	2773	736	23.0	977	1790	0.20
Maximum	4598	695	34.5	921	1992	0.36	4171	786	31.0	1497	2374	0.31
F value genotype	4.60***	1.58ns	2.93***	4.53***	1.68*	1.52ns	11.53***	2.84ns	2.63ns	3.36*	1.50ns	2.31ns
KS85W663-11-8/Lamar (11)												
Mean	3702	652	31.6	503	1975	0.21	3876	785	29.6	1140	2394	0.25
Minimum	2758	583	22.5	329	1442	0.15	3309	741	25.5	919	2026	0.18
Maximum	4671	702	38.0	723	2355	0.44	4407	814	32.5	1374	3039	0.30
F value genotype	5.18***	2.39**	4.55***	3.45***	3.00***	6.98***	5.57**	9.30***	4.74*	7.23**	5.30**	1.97ns
KS85W663-11-1/Lamar (18)												
Mean	3758	657	31.2	461	1810	0.22	4077	791	30.4	1034	2200	0.26
Minimum	3180	444	27.5	323	1319	0.16	3838	772	28.0	913	1900	0.25
Maximum	4533	698	32.0	744	2290	0.28	4364	815	32.0	1218	2471	0.28
F value genotype	2.05*	4.04***	3.75***	2.35*	2.40*	1.65*	1.80ns	2.21ns	6.93ns	20.25*	23.76*	1.28ns
KS87W822-2-1/Lamar (4)												
Mean	3826	668	30.3	514	1923	0.22	3983	792	28.8	1116	2372	0.24
Minimum	3236	618	24.5	329	1486	0.15	3158	764	25.5	897	1800	0.17
Maximum	4580	702	34.5	724	2384	0.29	4647	826	35.5	1294	3116	0.31
F value genotype	2.29**	1.38*	2.49**	2.35**	1.43ns	2.39**	9.99***	7.55***	9.74***	4.09**	3.82**	1.61ns

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

† number in parentheses indicates the number of derived lines for each population.

value of genotypes for kernel weight followed by the KS87W822-2-1/Lamar and Rio Blanco/Vista populations. The Arlin/Lamar and KS85W663-11-8/Lamar populations had the highest means among the populations for kernel weight.

The Rio Blanco/Lamar population had the highest F-value of genotypes for kernel number followed by the Arlin/Lamar and KS85W663-11-8/Lamar populations. The Rio Blanco/Vista population had the highest population mean followed by the Rio Blanco/Lamar and KS87W822-2-1/Lamar populations. The KS85W663-11-8/Lamar population had the highest F-value of genotypes for biomass among the populations followed by the Rio Blanco/Lamar population. The KS85W663-11-8/Lamar population had the highest population mean for biomass followed by the KS87W822-2-1/Lamar population. The KS85W663-11-8/Lamar population was the only population which had significant F-value of genotypes, and other populations had nonsignifcant F-values. However, the Rio Blanco/Vista population had the highest population mean among the populations followed by the Arlin/Lamar population (Table 8).

Populations with divergent parents (Arlin/Lamar, KS87W822-2-1/Lamar and KS85W663-11-8/Lamar) had higher means for all traits measured except for kernel number in the Rio Blanco/Vista and Rio Blanco/Lamar populations. The Rio Blanco/Vista population (cross between moderately dryland adapted parents) showed a wider range for grain yield, kernel number and biomass than the other populations (Table 8).

Table 8. Mean, minimum, maximum, and significance of genotype effects for grain yield, test weight, kernel weight, kernel number, biomass, and harvest index of five populations grown under chemical desiccation at Fort Collins averaged over 1998 and 1999.

Population	Grain yield	Test weight	Kernel weight	Kernel number	Biomass	Harvest index
	kg ha^{-1}	kg m^{-3}	mg $kernel^{-1}$	kernels m^{-2}	g m^{-2}	
Arlin/Lamar (16)†						
Parent mean	3516	748	304	676	1945	0.26
Population Mean	3791	733	30.6	724	1961	0.27
Population Minimum	3248	709	25.5	571	1708	0.20
Population Maximum	4349	757	33.8	882	2124	0.36
F value of genotypes	6.29***	7.47***	2.68*	7.19***	1.09ns	1.71ns
Rio Blanco/Lamar (9)						
Parent mean	3556	731	27.6	890	2035	0.28
Population Mean	3651	717	28.0	869	1952	0.25
Population Minimum	2851	679	25.5	661	1741	0.21
Population Maximum	4117	744	31.5	955	2207	0.34
F value of genotypes	27.58***	9.30***	3.30*	8.00***	3.03*	2.12ns
Rio Blanco/Vista (10)						
Parent mean	3543	704	27.2	979	1706	0.28
Population Mean	3614	713	29.0	970	1871	0.31
Population Minimum	2154	672	26.3	730	1590	0.23
Population Maximum	4210	733	32.5	1105	2081	0.52
F value of genotypes	6.63***	2.40ns	3.44*	4.34**	2.14ns	2.27ns
KS85W663-11-8/Lamar (11)						
Parent mean	4055	739	29.2	781	2107	0.25
Population Mean	3737	715	30.6	818	2136	0.25
Population Minimum	3260	676	25.5	677	1983	0.17
Population Maximum	4363	744	34.3	991	2438	0.48
F value of genotypes	3.57**	3.24*	11.44***	6.68***	3.61**	4.20**
KS87W822-2-1/Lamar (18)						
Parent mean	3897	740	28.9	796	2226	0.26
Population Mean	3949	731	29.4	827	2182	0.26
Population Minimum	3476	715	27.0	739	1890	0.20
Population Maximum	4520	758	33.0	973	2523	0.50
F value of genotypes	6.09***	3.07**	4.55***	2.80**	1.53ns	1.62ns

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

† Number in parentheses indicates the number of derived lines for each population.

Relationship between populations under desiccation and parents under desiccated and dryland conditions showed that all population means for grain yield test weight, kernel weight, kernel number and biomass were numerically higher than means of parents. Ranges of lines in each population were also higher than one or both parents for each population. As significant variability was observed for most traits among lines within populations, progress through selection should be effective.

Standardized genotypic variance estimates for traits were measured under chemical desiccation within the five populations to characterize and compare traits among the populations (Table 9). Standardized variances ranged from non-significant for kernel number in the Rio Blanco/Lamar population to 0.89±0.45 for grain yield in the same population. In each population, several traits with non-significant variances were observed.

The Rio Blanco/Lamar population showed large standardized genotypic variance estimates for 3 of 5 traits while the Arlin/Lamar population showed low to intermediate estimates for most traits. The large standardized variances among lines for grain yield, test weight and biomass in the Rio Blanco/Lamar population was because of segregants with low yield, test weight and biomass, rather than transgressive segregates with higher values for these traits (Table 8). Among the traits measured, kernel weight showed the highest standardized variance among the populations (0.59 average) for the four significant population variances.

Table 9. Standardized genotypic variance components for grain yield, kernel weight, kernel number, test weight, and biomass of five winter wheat populations grown under chemical desiccation at Fort Collins in 1998 and 1999.

	Standardized variance[†] (adjusted standard error of standardized variance)				
	Arlin/Lamar	Rio Blanco/Lamar	Rio Blanco/Vista	KS85W663-11-8/Lamar	KS87W822-2-1/Lamar
Number of lines	16	9	10	11	18
Grain yield	0.42 (0.40)	0.89 (0.45)	0.61 (0.46)	NS	0.45 (0.37)
Kernel weight	0.52 (0.28)	NS	0.61 (0.38)	0.77 (0.43)	0.65 (0.27)
Kernel number	0.45 (0.39)	NS	0.60 (0.67)	0.45 (0.43)	NS
Test weight	NS	0.66 (0.47)	NS	0.52 (0.32)	NS
Biomass	NS	0.77 (0.45)	NS	NS	NS

[†] Standardized genotypic variance component calculated as a ratio of the expected mean square of genotypes to the sum of expected mean square for genotype, genotype x year interaction, and error.

Kernel number showed the lowest standardized variance among the populations (0.45 average) for the two significant variances among the populations. The average standardized variances for test weight and biomass across populations were similar. Standardized genotypic variance was significant for both grain yield and kernel weight for all of the populations, with the exception of the KS85W663-11-8/Lamar population for grain yield and the Rio Blanco/Lamar population for kernel weight (Table 9). Variance estimates for test weight were only significant for the Rio Blanco/Lamar and KS85W663-11-8/Lamar populations while variance estimates for kernel number were significant only for the Arlin/Lamar and KS85W663-11-8/Lamar populations. Small and different variance components among lines for the five populations under desiccation with parents differing for drought tolerance and adaptation was not unlikely because of the lack of consistency in desiccation injury and lack of association of traits between dryland and desiccation conditions. However, selection in populations that showed significant genetic variation among lines and large standardized variances among lines should result in progress from selection (Tables 8 and 9).

None of the populations showed significant genetic variation across all variables tested. For example, the Rio Blanco/Lamar population showed high variation for grain yield but did not show variation for kernel number or kernel weight. The low amount of genetic variation of the population for traits could be due to the small number of lines considered within the populations.

Summary and Conclusions

In this study, entries responded differently under control, chemical desiccation, and dryland production conditions. Significant variation in desiccation injury was also observed for most variables examined. Variation among entries was also observed for chemical desiccation injury. Two types of entry response were observed: entries that performed well under chemical desiccation (e.g., had low desiccation injury) and entries that had high desiccation injury but performed well due to their higher potential. No consistent patterns were observed between years for chemical desiccation tolerance. A significant correlation was observed between grain yield injury and biomass injury, suggesting that improvements in grain yield may be realized through higher biomass at maturity. However, no significant correlations were observed between grain yield and desiccation injury. Significant differences among entries were observed under dryland conditions. Entries differed between dryland conditions and chemical desiccation while mean performance under dryland conditions was higher for test weight, kernel number, and harvest index. No significant associations were observed between dryland grain yield and either grain yield injury or kernel weight injury under chemical desiccation. The lack of association may be due to the relatively lower injury by chemical desiccation. The difference between dryland and fully irrigated kernel weight was moderately associated with grain yield injury and kernel weight injury, suggesting that the average stress level under dryland conditions was not sufficient to reveal differences in grain filling patterns among entries. Chemical desiccation

appeared to be inconsistent in differentiating crosses and parents while no correlation with dryland results was apparent.

Means ranges, and variances were used to characterize populations of derived-lines and compare traits under chemical desiccation. Because, non significant and small in variance components among lines for the five populations under desiccation with parents differing for drought tolerance and adaptation was expected. However, selection in those populations that showed significant genetic variation, based on the F test for genotypes and large standardized variances, should result in some progress from selection. Lack of consistent chemical injury response by populations and association between chemical desiccation and dryland conditions suggest that additional research is necessary to identify strategies and techniques to successfully exploit the chemical desiccation method in applied wheat breeding programs.

NONSTRUCTURAL CARBOHYDRATE ACCUMULATION AND REMOBILIZATION IN WINTER WHEAT

Abstract

In wheat (*Triticum aestivum* L.) and other small grains, the contribution of current assimilate to grain weight is often reduced due to the effect of various biotic and abiotic stresses. Therefore, an important source of carbohydrates for grain filling is nonstructural carbohydrates (NSC) stored in the stem. Information on genetic variation in stem NSC, and its remobilization to developing grains under chemical desiccation, is scarce. The objectives of this study were to characterize NSC concentration and remobilization among F_2-derived lines and their parents, determine associations among NSC measurements, and estimate genotypic variance components of NSC measurements under chemical desiccation. $F_{2:4}$ lines developed from six crosses with seven contrasting parents were planted under irrigation in a split- plot design with two replicates in 1998 and 1999 at Fort Collins, CO. Sodium chlorate ($NaClO_3$, 2% W:V, 125 mL m^{-2}) was applied to desiccated subplots 15 d postanthesis. Nonstructural carbohydrate concentration was determined from stem samplings made at 14 d postanthesis and at maturity in both the control and desiccated subplots. Significant variation among entries was observed for NSC concentration at the postanthesis sampling and at maturity in both the control and desiccated treatments. Very little consistency among entries was observed for NSC

measurements across entries and years. Stem NSC concentration at maturity was lower under desiccation than in the control treatment, suggesting that chemical desiccation increased utilization of stored NSC. Stem NSC concentration at the postanthesis was positively correlated with NSC remobilization during grain filling in the desiccated ($r=0.90$, $P<0.001$) treatment suggesting that the size of the NSC pool available at the onset grain filling is important for kernel growth. Correlation among grain yield and yield components and variables related to stem NSC showed very few significant associations. Genetic variance estimates showed that significant genetic variation in NSC concentration and remobilization was present among the populations tested. Selection within populations showing higher variance estimates should provide better progress for improvement of NSC parameters.

Introduction

In wheat and other small grains, current assimilation as a source of carbon for grain filling depends on photosynthetically active plant tissues after anthesis. This source is often limited due to the effect of biotic (plant pathogens) and abiotic (high temperatures, drought) stresses. In addition to reduced current assimilation during grain filling under stress, maintenance and respiration of live plant biomass also reduces the pool of available carbon for grain filling (Blum, 1998). Under such conditions, an important source of carbon for grain filling is stem nonstructural carbohydrate (NSC) reserves.

In wheat, an increase in stem NSC storage that occurs when spike demand is reduced by grain removal is associated with reduced translocation rates and a higher concentration of sugars in the sieve elements (Wardlaw and Moncur, 1976; Fisher and Gifford, 1987). Gallagher et al. (1976) studied grain growth patterns of field grown winter wheat under drought stressed and nonstressed conditions. In their study, the fraction of final grain weight from translocation of material assimilated before anthesis was greater (>50% vs. 35%) when conditions during grain filling were adverse for photosynthesis.

Stem NSC accumulation and storage capacity is strongly influenced by growing conditions at and before anthesis. Total stem NSC at anthesis was shown to vary from 50 to 350 g kg^{-1} dry matter in several different experiments (Asana and Basu, 1963; McCaig and Clarke, 1982; Davison and Chevalier, 1992; Kiniry, 1993).S tored NSCs were less in stressed (641 mg g^{-1}) than irrigated wheat (1047 mg g^{-1}) (Davison and Chevalier, 1992). Under dryland field conditions, only half the amount of nonstructural soluble carbohydrates was available for remobilization during grain filling compared with irrigated conditions. Stem length is important in affecting stem reserve storage. The dwarfing genes of wheat were found to reduce reserve storage by 37%, as a consequence of a 21% reduction in stem length (Borrel et al., 1993). However, examination of stem reserves in wheat by Rawson and Evans (1971) failed to show any differences in NSC utilization between tall and short cultivars. Similarly, Austin et al. (1980) found no evidence for genetic differences in stem NSC contribution to grain weight of 24 dwarf and tall barley (*Hordeum vulgare* L.) lines.

Stem NSC remobilization and contribution to final grain weight can be influenced by both cultivar and environment. Demand by the developing grains (sink) is a primary factor in determining stem reserve remobilization (Blum, 1998). When degraining reduced sink size, more reserves were stored in the stem compared with intact spikes (Kuhbauch and Thorne, 1989). The interaction between sink size and the demand for stem NSC appears to depend on the environment before and during grain filling (Bonnett and Incoll, 1992a). Shading of barley plants after anthesis promoted the remobilization of stem reserves for grain filling (Bonnett and Incoll, 1992a). When wheat plants were shaded during grain filling, up to 0.93 g of grain was produced per g of assimilates exported from the stem (Kiniry, 1993). Stem NSC remobilization is also affected by the presence and rate of development of water deficits during the grain filling period. Palta et al. (1994) found that total grain carbon with rapid development of water deficits was reduced 24% relative to slow water deficit development. In their study, postanthesis assimilation was reduced 57%, while remobilization of NSC reserve was increased 36%. Therefore, it is not surprising that estimates of the relative contribution of stem NSC to final grain weight vary widely (Blum, 1998) and in fact the estimates from the literature range from 6% to 100% (Austin et al., 1980; Pheloung and Siddique, 1991; Davidson and Chevalier, 1992; Borrell et al., 1993; Blum et al., 1994; Palta et al., 1994).

Improving grain filling capacity is an important breeding target in cereals subjected to biotic and abiotic stresses during grain filling (Blum, 1998). Genotypic variation exists for various aspects of grain filling. The capacity for

accumulating large stem NSC pools appears to be a genetically controlled, constitutive trait (Blum et al., 1994; Hunt, 1979), which may be linked to assimilate partitioning during stem elongation and morphological development of the stem. If greater stem partitioning is the basis for high reserve storage it might perhaps be at the expense of grain yield potential. Pheloung and Siddique (1991) found that the higher yielding cultivars had less reserve storage and suffered greater reductions in grain yield under drought stress during grain filling compared with the lower yielding cultivars. Similarly, Hossain et al. (1990) showed that modern wheat cultivars were less capable of grain filling from stem reserves than older wheat cultivars. Blum et al. (1989) showed that landraces were more efficient at grain filling from stem reserves than a modern high yielding cultivar, even though this advantage could also be ascribed to the taller stature of the landraces. Alternatively, other studies in wheat have not observed a negative correlation between yield potential and NSC reserve contribution for grain filling (Blum et al., 1994; Davidson and Birch, 1992). However, cultivars with better tolerance to stress during grain filling must have the capacity for high stem reserve storage, if necessary even at the expense of a reduction in yield potential (Blum, 1998).

Use of NSC storage for grain filling was found to be proportional to the size of NSC storage in winter wheat cultivars (Hunt, 1979). Nicolas and Turner (1993) found that increased grain filling under stress was proportional to stem NSC concentration at flowering across different wheat cultivars. However, some wheat cultivars had sufficient NSC storage but were lacking in their ability to

remobilize the NSC to the grain (Hossain et al., 1990). Remobilization and utilization of the NSC reserves depends also on demand by the sink (Blum, 1998). While there may be genetic variability in enzymatic activity involved with remobilization, such activity may also be a function of demand and substrate concentration (Dubois et al., 1990). The capacity to deposit starch in the kernel endosperm under heat stress is another potential source imbalance. While the size of NSC storage is important, the size of the sink and the capacity to utilize the imported carbon are also important for allowing grain filling from stem NSC (Blum, 1998; Hay and Walker, 1989).

Blum et al. (1983a, b) and Blum (1998) proposed the use of a contact chemical desiccant (magnesium chlorate or sodium chlorate) applied to the canopy after anthesis to reveal the capacity for grain filling by stem reserves. Similarly, Nicolas and Turner (1993) confirmed the use of chemical desiccation (potassium iodide) as a means for detecting genetic variation in grain filling from stem reserves in wheat.

Information on genetic variation in stem NSC storage and utilization under chemical desiccation in wheat breeding populations is lacking, particularly in derived-line populations developed from crosses with parents contrasting in overall drought stress tolerance. The objectives of this study were therefore to:

1) determine if NSC concentration and remobilization is greater under chemical desiccation than under fully-irrigated, non-desiccated conditions;

2) estimate the correlation between NSC concentration and remobilization important agronomic characteristics; and

3) estimate the magnitude of genotype variance relative to the genotype x environment interaction and error variance components for NSC concentration and remobilization under chemical desiccation and fully-irrigated, non-desiccated conditions.

Materials and Methods

Line derivation and field experiment layout

All field studies conducted during this experiment were done at the Colorado State University Agricultural Research Development and Education Center (ARDEC) at Fort Collins, CO. In 1994, crosses were made in the greenhouse among eight hard red winter and hard white winter wheat genotypes including, 'Arlin', 'Rio Blanco', 'Vista', 'Lamar', 'KS85W663-11-1', 'KS85W663-11-8', and 'KS87W822-2-1'. Lamar, Vista, and Rio Blanco are wheat cultivars with good adaptation for dryland production in the west-central Great Plains while Arlin, KS85W663-11-8, KS85W663-11-1 and KS87W822-2-1 are genotypes that have shown drought stress symptoms under dryland conditions in eastern Colorado (Dr. J.S. Quick, personal communication).

In 1995-1996 F_2 populations from the six crosses Arlin/Lamar, Rio Blanco/Lamar, Rio Blanco/Vista, KS85W663-11-8/Lamar, KS85W663-11-1/Lamar, and KS87W822-2-1/Lamar were space planted in a field nursery. Head selections were made and $F_{2:3}$ head rows were grown in the field in 1996-1997 and rows with good visual appearance were harvested in bulk. Two hundred and

eighty eight $F_{2:4}$ derived lines (48 lines per population) were grown in the field study in 1997-1998 (1998 season) along with the seven parent genotypes. Sixty eight $F_{2:4}$ lines (four to eighteen lines per population) chosen to represent a broad range of performance characteristics in 1998, were grown in the field study in 1998-1999.

Field experiments were planted under full irrigation on 27 September 1997 (1998 season) and 28 September 1998 (1999 season). Field plots were planted in rows 3.4 m long on two raised beds 0.76 m apart; two rows 20 cm apart were planted on each bed (experimental unit 5.2 m^2). The average seeding rate was 50 kg ha^{-1}. Derived lines and parents were planted in a split-plot arrangement in a randomized complete block design with two replicates. Entries (derived lines and parents) were considered as main plots and treatments (chemical desiccation and control) as subplots. Sodium chlorate ($NaClO_3$, 2% W:V, 125 mL m^{-2}) was applied to the appropriate subplot 15 days postanthesis with a CO_2-propelled backpack spray apparatus.

Nonstructural carbohydrate determination

Partitioning of NSC in stems and leaf sheaths was monitored by sampling plants from the field experiments. Six randomly selected main tillers from the control subplot were cut at the ground level 14 days postanthesis and one day before the chemical desiccant was applied. Four main tillers from each subplot (desiccation and control) were cut at maturity prior to harvest. Collected samples were placed in paper bags and immediately dried at 38 °C for 72 h. After drying, leaves and spikes were separated from the stems and leaf sheaths. Stem and

sheath samples were then ground (Retsch GmbH grinder, Haan, Germany) to pass a 1-mm screen and stored in plastic bags. Extraction and determination of NSC from the samples was done using the anthrone reagent method of Yemm and Willis (1954) as follows.

Ground stem tissue samples of 0.15 to 0.20 g dry weight transferred to 25 mL Ehrlenmeyer flasks. Absolute ethanol (1.5 mL) was then added to each flask followed by the addition of 12.5 mL of deionized water. Flasks were secured in an incubator-shaker and agitated for 2 h at 60°C. Samples were removed and the contents were passed through a plastic funnel with a Whatman #541 filter paper using deionized water as a rinsing agent. Each extract (0.5 mL) was then transferred to a 16 mm x 115 mm culture tube to which 0.5 mL of deionized water was then added. At the same time, 1.0 mL of each sugar standard was transferred to separate culture tubes. Standards were prepared from 1.0, 2.0, 3.0, and 6.0 mL of stock solutions where each stock solution was prepared using 2 g fructose sugar and deionized water. To each culture tube, 10 mL of cold anthrone solution (72% H_2SO_4, anthrone reagent, and thiourea) was then added. After briefly vortexing, tubes were covered with plastic wrap and placed in a tube rack in a 95° C water bath for 30 min. To stop the reaction between the anthrone and the sugar from the plant tissue, the rack was removed from the water bath and placed in an ice bath for 5 min. The contents of each tube were then gently agitated prior to transfer of a small aliquot (approximately 0.20 mL) to separate small cuvettes (approximately half full). Using a spectrophotometer, the percent transmission at 625 nm was then recorded. A standard curve prepared from

transmission values of the known sugar solutions was used for determination of NSC concentration of the test samples. NSC remobilization was determined from difference of NSC concentration at the postanthesis and NSC concentration at maturity.

Data analysis

Proc GLM in SAS was used for analysis of variance (ANOVA) for each variable to compare NSC concentration and remobilization, and estimate the magnitude of genotypic variance for these traits. Fischer's protected Least Significant Difference (LSD) was used to compare genotype and treatment means for measured variables. Simple Pearson Correlation coefficients were calculated using between treatment means and the Proc CORR procedure of SAS.

The magnitude of the genotypic variance among lines within a family was estimated based on components of variance from the ANOVA as described in Fehr (1987) and Hallauer and Miranda Filho (1988). Both trial year and genotypes were considered as random effects in the model. Each population was analyzed independently. The genotypic variance component (σ^2_g) was estimated assuming that the variance among inbred lines is equal to to the expected mean mean squares for the geotype x environment (year) interaction minus the expected mean square for genotypes divided by the number of years and number of replications (Hallauer and Miranda Filho, 1988):

$$\sigma_g^2 = \frac{(MS_g - MS_{gxe})}{ry}$$

where MS_g is the mean square of genotype effects, MS_{gxe} is the mean square of genotype x environment effects, r is the number of replications within each location; and y is the number of years. Similarly, the variance for the genotype x environment interaction effect was calculated as:

$$\sigma^2_{gxe} = \frac{\left(MS_{gxe} - MS_{error}\right)}{r}$$

The size of the variance component for each trait is dependent on the units of measure for the trait. Therefore, it is necessary to standardize the variance components as a fraction of the total or non-environmental variation (year and replication in this experiment) prior to comparison of values (Basset et al., 1989; Graybosch et al., 1996). Genotypic variance was standardized as a percent of the total non-environmental variation using the formula:

$$\text{Standardized } \sigma^2_g = \frac{\sigma^2_g}{[(\sigma^2_g + \frac{\sigma^2_{gxe}}{y}) + (\frac{\sigma^2_{error}}{ry})]}$$

The standard errors for the standardized variance among genotypes were estimated from the ANOVA as:

$$SE\ \sigma^2_g = \sqrt{\frac{2}{(re)^2} x (\frac{M_4^2}{n+1} + \frac{M_3^2}{(e-1)(n-1)+2})}$$

where r is the number of replications within an environment, e is the number of environments, M_3 is the genotype x environment interaction mean square, and M_4 is the genotype mean square (Hallauer and Miranda Filho, 1988).

Results and Discussion

Nonstructural carbohydrate concentration

To determine differences among NSC components measured, a combined ANOVA over years was conducted after confirming homogeneity of error variance using Bartlett's test (Gomez and Gomez, 1984). Stem NSC concentration was consistent among entries between years for both the postanthesis and harvest sampling in the desiccated treatment (Table 1). Differences among entries were observed, however, between years for the harvest sampling from the control treatment where 33% more NSC remained in the stems in 1998 than in 1999 (72.1 vs. 54.1 mg g^{-1}). The difference between years in unmobilized stem NSC may have been due to environmental differences, especially high maximum air temperature during the grain filling period in 1998.

Significant ($P<0.01$) differences in stem NSC concentration among entries (parents and derived lines) and samplings were observed in both years of the study (Table 1). Average NSC concentration at the postanthesis sampling was much greater than that observed at maturity in either the control (76% less) or desiccated (87% less) treatments. For most entries in both years, harvest NSC concentration was lower in the desiccated treatment than in the control treatment, with the exception of the Rio Blanco/Lamar population, which showed slightly higher NSC concentration in the desiccated treatment than in the control treatment.

Table 1. Stem nonstructural carbohydrate concentration at the 14 days postanthesis and maturity (control and desiccated) sampling periods at Fort Collins, CO, in 1998 and 1999.

Genotype	1998			1999		
		Maturity			Maturity	
	Postanthesis	control	desiccated	Postanthesis	control	desiccated
	——— mg g^{-1} ———			——— mg g^{-1} ———		
Parent						
Arlin	267.7	89.4	34.6	265.0	67.2	30.5
Lamar	256.9	24.3	17.0	234.5	44.5	14.3
Rio Blanco	303.5	80.6	36.9	300.0	63.2	22.1
Vista	304.8	107.9	32.0	284.4	22.3	15.1
KS85W663-11-8	222.8	87.1	33.8	256.5	54.0	42.0
KS85W663-11-1	253.8	47.3	33.6	283.5	74.2	48.1
KS87W822-2-1	275.8	79.5	60.0	267.2	63.3	42.5
Derived line						
Arlin/Lamar (16)	250.6	50.7	29.1	255.3	40.4	28.0
Rio Blanco/Lamar (9)	251.3	65.7	29.1	259.1	47.8	51.4
Rio Blanco/Vista (10)	293.5	83.0	46.5	299.0	55.8	37.0
KS85W663-11-8/Lamar (11)	246.1	78.7	34.5	266.1	62.0	40.9
KS85W663-11-1/Lamar (4)	254.6	74.1	38.5	274.2	58.0	49.2
KS87W822-2-1/Lamar (18)	241.5	68.8	35.8	260.5	50.3	38.5
Mean	263.8	72.1	35.5	269.7	54.1	35.3
CV (%)						
Entry		13			10	
Treatment		18			16	
LSD (0.05)						
Entry		24.8			16.0	
Treatment		11.9			7.7	

The general pattern of reduced NSC concentration at maturity observed under chemical desiccation, relative to the adjacent control treatment, is consistent with previous field studies that examined changes in stem NSC concentration following chemical desiccation (Blum et al., 1983b; Davidson and Chevalier, 1992).

There appeared to be little consistency in NSC concentration among entries and between years at any of the three sampling periods. However, the cultivar Lamar, a known dryland-adapted cultivar, appeared to rely on stem NSC to a greater extent than other entries in the study, particularly known drought-susceptible entries such as Arlin, KS85W663-11-1 and -8 (both sister selections of the cultivar 'Heyne'), and KS87W822-2-1. Vista, another cultivar with a good performance record in dryland trials, was less consistent between years for NSC concentration, with low NSC concentration at maturity in the desiccated treatment in 1999 but not in 1998. Compared with groups of derived lines, parents showed a generally wider range of NSC concentrations at each of the three sampling periods.

NSC remobilization

No significant differences were observed between 1998 and 1999 for NSC remobilization. In a combined analysis over years, significant differences in stem NSC remobilization were observed among entries (parents and derived lines) and treatments (Table 2). Averaged across both years, NSC remobilization was 14% more under chemical desiccation than under the control treatment. No clear

pattern was observed, however, between parent entries differing in relative drought stress tolerance or susceptibility. Parent entries known for good performance under dryland conditions (e.g., Lamar, Vista, Rio Blanco) appeared to show no greater NSC remobilization under desiccated conditions. As with NSC concentration, a wider range in NSC remobilization was observed among parent entries than groups of derived lines. In fact, in several instances (e.g., Arlin/Lamar, Rio Blanco/Lamar, and RioBlanco/Vista populations) NSC remobilization for groups of derived lines was less than either of the two parents used in the cross.

Demand by developing grains, as a primary carbohydrate sink, is a primary factor in determining stem reserve remobilization (Blum, 1998). The underlying premise of chemical desiccation is that increased stem NSC remobilization occurs in response to decreased canopy photosynthesis. Therefore, under this situation, grain growth may thus be described as being both sink limited (from anthesis to the beginning of the linear phase of kernel growth) and source limited (from the linear phase of kernel growth to maturity (Borrell et al., 1989).

No clear differences in remobilization were observed between groups of known drought-tolerant and drought-susceptible parent entries. For example, Lamar and KS85W663-11-1 showed very similar values for both NSC remobilization yet they have very contrasting responses to even moderate drought stress conditions in the field.

Table 2. Stem nonstructural carbohydrate (NSC) remobilization between the postanthesis and maturity sampling periods at Fort Collins, CO, in 1998 and 1999.

Genotype	NSC Remobilization		
	control	desiccated	difference[+]
Parent	-------- mg g^{-1}--------		--- % ---
Arlin	188.4	234.2	24
Lamar	211.4	230.1	9
Rio Blanco	229.8	272.2	18
Vista	229.5	271.1	18
KS85W663-11-8	169.1	201.7	19
KS85W663-11-1	207.9	227.9	10
KS87W822-2-1	200.1	220.1	10
Derived line			
Arlin/Lamar (16)[‡]	207.4	224.5	8
Rio Blanco/Lamar (9)	198.5	214.9	8
Rio Blanco/Vista (10)	226.8	254.5	12
KS85W663-11-8/Lamar (11)	185.8	218.4	18
KS85W663-11-1/Lamar (4)	198.4	220.6	11
KS87W822-2-1/Lamar (18)	191.4	213.9	12
Mean	203.4	231.1	14
CV (%)			
Entry	17		
Treatment	8		
LSD (0.05)			
Entry	38.1		
Treatment	15.0		

[+] Percent difference between the control and desiccated treatments.
[‡] Number in parentheses indicates the number of derived lines for each population.

In previous studies (Blum et al., 1989), landraces of wheat were more efficient at grain filling from stem reserves than modern high yielding cultivars. This trend was also noted by Hossian et al. (1990), where newer cultivar releases were less capable of grain filling from stem reserves than older cultivars. Genotypes with better dryland performance have usually shown greater NSC remobilization than genotypes known for greater drought stress susceptibility. The reason for the lack of this association in this study may be due to differences in grain filling capacity of the genotypes used.

Trait associations

Nonstructural carbohydrates, and their pattern of remobilization during grain filling, are highly complex. Furthermore, the relationship between NSC concentration and remobilization and grain yield and other attributes is not fully understood. Variability in grain yield cannot be attributed to a single physiological or morphological feature of plant growth. It is thus useful to investigate the correlation between NSC traits and grain yield in order to evaluate the potential for use of NSC determinations as screening tools in breeding program.

Stem NSC concentration at the postanthesis sampling was not associated ($P>0.05$) with NSC concentration at maturity under either the control or desiccated treatment (Table 3). This lack of association suggests that stem NSC at maturity is generally not a function of the pool of stem NSC present at the onset of grain filling. Stem NSC concentration at maturity, in both the control and desiccated treatments, was also uncorrelated with NSC remobilization.

Stem NSC concentration at the postanthesis sampling was positively correlated with NSC remobilization during grain filling in both the control ($r=0.81$, $P<0.01$) and desiccated ($r=0.90$, $P<0.001$) treatments (Table 3). The strength of this association was greater in the desiccated treatment than in the control treatment, suggesting that the size of the NSC pool available at the onset of grain filling is more important under conditions that limit photosynthesis during grain filling, as is the case under chemical desiccation. Similarly, Nicolas and Turner (1993) found that grain filling under postanthesis stress was proportional to stem NSC concentration at flowering across different wheat cultivars.

Nonstructural carbohydrate remobilization in the control treatment was positively associated ($r=0.88$, $P<0.001$) with NSC remobilization in the desiccated treatment (Table 3). This association highlights the importance of stem NSC remobilization for grain filling, even though demand by the developing sink is the primary factor that influences stem NSC remobilization (Blum, 1998). Correlations among grain yield, yield components (e.g., kernel weight and kernel number), and variables related to stem NSC were estimated to further understand the grain filling process under the control and desiccated treatments. Very few significant correlations were observed between stem NSC concentration and the other measured variables (Table 4). The most notable correlations were those observed between NSC concentration at the postanthesis sampling and kernel number in the control treatment ($r=0.61$, $P<0.05$) and kernel weight ($r=-0.58$, $P<0.05$) and biomass ($r=-0.61$, $P<0.05$) in

Table 3. Pearson correlation coefficients among stem nonstructural carbohydrate (NSC) concentration at 14 days postanthesis and maturity (control and desiccated), remobilized stem NSC during grain filling at Fort Collins, CO, in 1998 and 1999.

	Stem NSC concentration at			Remobilized stem NSC from postanthesis to maturity at	
		maturity			
	postanthesis	control	desiccated	control	desiccated
Stem NSC concentration					
control (maturity)	0.44				
desiccated (maturity)	0.02	0.56*			
Remobilized stem NSC					
control	0.81**	-0.18	-0.34		
desiccated	0.90***	0.17	-0.41	0.88***	

*, **, *** Significant at 0.05, 0.01, and 0.001 probability levels, respectively. (n =13)

the desiccated treatment. These correlations suggest that genotypes with higher intrinsic ability to accumulate NSC prior to grain filling tend to show reduced kernel weight and biomass when treated with the chemical desiccant. This observation is contradictory to the general principle of chemical desiccation where NSC are supposed to help maintain kernel weight under conditions that limit photosynthesis during grain filling. With regard to stem NSC remobilization, a similar pattern was evident as very few significant correlations were observed (Table 4).

Remobilized NSC of the populations under control and desiccated treatments is shown in Table 5. Under the control treatment, all populations except the KS87W822-2-1/Lamar population had remobilized NSC values within the range of parents. Under the desiccated treatment, all populations except the Arlin/Lamar population showed low values of remobilized NSC relative to their parents. Remobilized NSC was positively correlated with kernel number under both the control ($r=0.67$, $P<0.05$) and desiccated ($r=0.58$, $P<0.05$) treatments, suggesting that kernel number maintenance was dependent on the capacity to remobilize NSC either with or without reduced photosynthesis during grain filling.

Genotypic variance

The five populations evaluated represent crosses between divergent parents for overall dryland adaptation. The populations responded differently for nonstructural carbohydrate (NSC) measurements (Table 5). At the postanthesis sampling, the KS85W663-11-8/Lamar and KS87W822-2-1/Lamar populations

Table 4. Pearson correlation coefficients between nonstructural carbohydrate measurements and grain yield, kernel number, kernel weight, biomass, and harvest index at Fort Collins, CO, in 1998 and 1999.

	Grain Yield		Kernel Number		kernel weight		biomass		harvest index	
	control	desiccated	control	desiccated	control	desiccated	control	desiccated	control	desiccated
Stem NSC concentration										
Postanthesis	-0.46	-0.37	0.61*	0.54	-0.39	-0.58*	-0.54	-0.61*	0.15	0.36
control (maturity)	0.22	-0.09	0.25	-0.11	-0.32	-0.46	-0.61*	-0.56*	0.33	0.45
desiccated (maturity)	-0.37	0.33	0.03	0.21	-0.28	-0.35	-0.07	-0.06	0.19	0.19
Remobilized stem NSC										
control	-0.35	-0.35	0.50	0.67*	-0.22	-0.34	-0.19	-0.30	0.05	0.10
desiccated	-0.26	-0.48	0.55	0.58*	-0.24	-0.39	-0.46	-0.53	0.22	0.25

*, ** Significant at 0.05 and 0.01 probability levels, respectively. (n=13)

Table 5. Mean, minimum, maximum, and significance of genotype carbohydrate (NSC) measurements of five populations grown at effects for nonstructural carbohydrate, Fort Collins in 1998 and 1999.

Population	NSC Concentration			Remobilized Stem NSC	
		Maturity			
	postanthesis	control	desiccated	control	Desiccated
	mg g^{-1}				
Arlin/Lamar (16) †					
Mean	257	49	27.0	208	230
Minimum	229	28	17.0	187	189
Maximum	319	79	47.0	256	290
F value of genotype	2.42*	1.45ns	1.34ns	1.02ns	2.86**
Rio Blanco/Lamar (9)					
Mean	254	59	44.0	194	210
Minimum	231	49	29.0	163	165
Maximum	283	83	66.0	225	235
F value of genotype	4.36**	2.33ns	1.00ns	3.34*	2.57ns
Rio Blanco/Vista (10)					
Mean	300	74	49.0	226	251
Minimum	265	32	23.0	184	286
Maximum	323	123	86.0	269	217
F value of genotype	2.16ns	2.86*	2.52*	1.54ns	1.87ns
KS85W663-11-8/Lamar (11)					
Mean	259	77	41.0	182	218
Minimum	245	47	23.0	139	191
Maximum	281	116	68.0	209	237
F value of genotype	1.56ns	6.45***	2.21ns	3.83**	1.02ns
KS87W822-2-1/Lamar (18)					
Mean	252	60	37.0	192	215
Minimum	218	44	25.0	151	174
Maximum	278	79	58.0	216	245
F value of genotype	24.9*	0.82ns	0.87ns	1.35ns	1.67ns

*, **, *** Significant at 0.05,0,01, and 0.001 probability levels, respectively; ns = non significant.
† Number in parentheses indicates the number of derived lines for each population.

had higher NSC concentration than their parents while the other populations were within the range of their parents. All the populations, except the KS85W663-11-8/Lamar population, had NSC concentration within the range of their parents at maturity under the control treatment. Under chemical desiccation, three populations (e.g., Rio Blanco/Lamar, Rio Blanco/Vista and KS85W663-11-8/Lamar populations) showed higher NSC concentration than their parents.

The Arlin/Lamar population had high NSC remobilization under both controlled and desiccated treatments and had the largest range for stem NSC concentration at postanthesis and NSC remobilization under desiccation among the populations evaluated (Table 5). The Rio Blanco/Vista population had the highest stem NSC concentration at the postanthesis sampling under desiccation and remobilization under both control and desiccated treatments. High NSC concentration at postanthesis, low concentration of NSC concentration at maturity and high concentration of remobilized stem NSC (especially under desiccated conditions) are established factors to indicate drought tolerance to wheat cultivars. Based on these factors, populations derived from the cross of cultivars adapted under dryland conditions in Colorado (e.g., Lamar, Rio Blanco, and Vista) showed better performance than the populations derived from crosses with the advanced lines KS85W663-11-8 and KS87W822-2-1.

Standardized genotypic variances for nonstructural carbohydrate concentration and remobilization under the control and desiccated treatments are shown in Table 6. Standardized variances ranged from non-significant for several

NSC parameters to 0.75±0.45 for NSC concentration at postanthesis and 0.75±0.51 for NSC concentration under irrigation (Table 6). In many cases, variances were non significant. This result was not unexpected given the relatively small population size of each of the crosses.

Large genotypic variances among lines for several traits were observed in the Rio Blanco/Vista and Rio Blanco/Lamar populations, both of which being crosses between parents with relatively better performance under dryland conditions. The Arlin/Lamar population, a cross between parents contrasting for dryland performance, had the lowest genotypic variances for several of the traits measured. While the Rio Blanco/Lamar population had large genotypic variance for NSC concentration at the postanthesis sampling, variances were much lower for NSC remobilization, because several lines had especially low means for these traits (Table 5). Genotypic variance for NSC concentration under desiccation was significant in only two populations while variance in NSC remobilization in the control treatment was only significant in one population. Crosses with Rio Blanco and Vista, both better performing under dryland conditions, showed higher standardized variance for all NSC measurements compared to the other crosses. Selection progress for measured traits should be expected in those populations that showed significant genotypic variation (based on the F test for genotypes, Tables 5 and 6).

Table 6. Standardized genotypic variance components for nonstructural carbohydrate (NSC) concentration and remobilization of five winter wheat populations grown at Fort Collins, CO, in 1998 and 1999.

	Standardized variance (adjusted standard error [+])				
Population	Arlin/Lamar	Rio Blanco/Lamar	Rio Blanco/Vista	KS85W663-11-8/Lamar	KS85W663-11-1/Lamar
Number of lines	16	9	10	11	18
Parameters					
NSC concentration					
Postanthesis	0.48 (0.30)	0.75 (0.45)	0.63 (0.53)	NS	0.66 (0.39)
Control	NS	0.34 (0.28)	0.75 (0.51)	0.48 (0.46)	NS
Desiccated	NS	NS	0.55 (0.41)	0.40 (0.32)	NS
NSC remobilized					
Control	NS	0.60 (0.39)	NS	NS	NS
Desiccated	0.53 (0.29)	0.45 (0.34)	0.52 (0.51)	NS	0.51 (0.49)

[+] Adjusted standard error, in parentheses, of the standardized genotypic variance estimates calculated as a ratio of the expected mean square of genotypes to the sum of expected mean square for genotype and genotype x year interaction effects.

Summary and Conclusions

Significant variation among entries and populations was observed for NSC concentration at all samplings in both the control and desiccated treatments. Stem NSC concentration at maturity was lower in the desiccated treatment than in the control treatment, suggesting that utilization of NSC stored in the stem was greater under chemical desiccation. Genotypic performance for NSC concentration was generally inconsistent across entries and years. Parents showed a wider range of stem NSC concentration than derived lines. No significant differences were observed for NSC remobilization. Nonstructural carbohydrate remobilization under desiccation was much higher than in the control treatment, further supporting previous observations that stem NSC are utilized to a greater extent when photosynthesis is limited or eliminated during grain filling.

Stem NSC concentration at the postanthesis sampling was positively correlated with NSC remobilization during grain filling in both control and desiccated treatments, suggesting that the size of NSC pool available at the onset of grain filling is more important under conditions that limit photosynthesis during grain filling. Correlation among grain yield and yield components and variables related to stem NSC showed very few significant associations. Remobilized NSC was positively correlated with kernel number under both the control and desiccated treatments, suggesting that kernel maintenance was dependent on the capacity to remobilize NSC during grain filling.

Means and variances were calculated within five populations to provide a characterization of populations and compare stem NSC concentration and remobilization at postanthesis, under control and desiccated treatments. Populations derived from Lamar, Rio Blanco, Vista, and Arlin were found to show better performance for NSC measurements than the populations derived from KS85W663-11-8 or KS87W822-1. The cross between Rio Blanco and Vista showed higher standardized variance across all NSC measurements than other crosses. Those parameters with significant variation based on the F test of genotypes and large variances are useful indicators for selection among the derived lines in the early stage.

REFERENCES

Adams, M.W. 1967. Basis of yield component compensation in crop plants with special references to the field bean, *Phaseolus vulgaris*. Crop Sci. 7:505-510.

Aggarwal, P.K., and S.K. Sinha. 1984. Effect of water stress on grain growth and assimilate partitioning in two cultivars of wheat contrasting in their yield stability in a drought-environment. Ann. Bot (London). 53:329-340.

Archbold, H.K. 1942. Physiological studies on plant nutrition. 13. Experiments with barley on defoliation on shading of ear in relation to sugar metabolism. Ann. Bot (London). 6:487-531.

Asana, R.D., and R.N. Basu. 1963. Studies in physiological analysis of yield. VI. Analysis of the effect of water stress on grain development in wheat. Ind. J. Physiol. 6:1-13.

Austin, R.B. 1992. Can we improve on nature? p. 29. *In* Abstracts. 1st Int. Crop Science Congress Ames, IA.

Austin, R.B. 1999. Yield of wheat in the United Kingdom: Recent advances and prospects. Crop Sci. 39: 1604-1610.

Austin, R.B., C.L. Morgan, M.A. Ford, and S.C. Bhagwat. 1982. Flag leaf photosynthesis of *Triticum aestivum* and related diploid and tetraploid species. Ann. Bot. (London), 49:177-199.

Austin, R.B., J. Bingham, R.D. Blackwell, L.T. Evans, M.A. Ford, C.L. Morgan, and M. Taylor. 1980. Genetic improvements in winter wheat yield since 1900 and associated physiological changes. J. Agric. Sci. (Cambridge) 94:675-689.

Austin, R.B., J.A. Edrich, M.A. Ford, and R.D. Blackwell. 1977. The fate of the dry matter, carbohydrates and ^{14}C lost from the leaves and stems of wheat during grain filling. Ann. Bot. (London) 41:1309-1321.

Austin, R.B., R.B. Morgan, M.A. Ford, and R.D. Blackwell. 1980. Contributions to grain yield from pre-anthesis assimilation in tall and dwarf barley genotypes in two contrasting seasons. Ann. Bot. (London) 45:309-316.

Baker, C.K., J.N. Gallagher, and J.L. Monteith. 1980. Day length change and leaf appearance in winter wheat. Plant Cell and Environ. 3:285-287.

Barlow, E.W.R., J.W. Lee, R. Munns, and M.G. Smart. 1980. Water relations of the developing wheat grain. Aust. J. Plant Physiol. 7:519-525.

Basset, L.M., R.E. Allan, and G.L. Rubenthaler. 1989. Genotype x environment interactions on soft white winter wheat quality. Agron. J. 81:955-960.

Begg, J.E., and N.C. Turner. 1976. Crop water deficits. Adv. Agron. 28:161-217.

Bernado, R. 2002. Breeding for quantitative traits in plant. p. 118-119. Breeding for quantitative traits in plants. Stemma press. Woodbury, MN.

Bidinger, F., R.B. Musgrave, and R.A. Fischer. 1977. Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley. Nature 270:431-433.

Blum, A. 1988. Plant breeding for stress environments. CRC Inc., Boca Raton, FL.

Blum, A. 1998. Improving wheat grain filing under stress by stem reserve mobilization. Euphytica 100:77-83.

Blum, A., B. Sinmena, J. Mayer, G. Golan, and L. Shpiler. 1994. Stem reserve mobilization supports wheat grain filling under heat stress. Aust. J. Plant Physiol. 21:771-781.

Blum, A., G. Golan, J. Mayer, B. Sinmena, and J. Burra. 1989. The drought response of landraces of wheat from the Northern Negev desert in Israel. Euphytica 43: 87-96.

Blum, A., H. Poiarkova, G. Golan, and J. Mayer. 1983b. Chemical desiccation of wheat plants as a simulator of post-anthesis stress. I. Effects on translocation and kernel growth. Field Crops Res. 6:51-58.

Blum, A., J. Mayer, and G. Golan. 1983a. Chemical desiccation of wheat plants as simulator of postanthesis stress. II. Relations to drought stress. Field Crops Res. 6:149-155.

Bonnett, G.D., and L.D. Incoll. 1992. Effects on the stem of winter barley of manipulating the source and sink during grain filling: Changes in the composition of water-soluble carbohydrates in internodes. J. Exp. Bot. 44: 83-91.

Borrel, A.K., L.D. Incoll, and M.J. Dalling. 1993. The influence of the *rht1* and *rht2* alleles on the deposition and use of stem reserves in wheat. Ann. Bot. 71:317-326.

Boyer, J.S., and H.G. McPherson. 1975. Physiology of water deficits. Cereal Crops. Adv. Agron. 27:1-23.

Bremner, P.M. 1972. Accumulation of dry matter and nitrogen by grains in different position of the wheat ear as influenced by shading and defoliation. Aust. J. Biol. Sci. 25:657-668.

Brocklehurst, P.A. 1977. Factors controlling grain weight in wheat. Nature 266:348-349.

Bruckner, P.L., and R.C. Frohberg. 1987. Rate and duration grain fill in spring wheat. Crop Sci. 27:451-455.

Calderini, D.F., M.P. Reynolds, and G.S. Slafer. 1999. Genetics gains in wheat yield and associated physiological changes during the twentieth century. p. 351 – 372. *In* E.H. Satore and G.A. Slafer (ed.) Wheat: Ecology and physiology of yield determination. Haworth Press Inc.,Binghamton, NY.

Carver, B.F., R.C. Johnson, and A.L. Rayburn. 1989. Genetic analysis of photosynthetic diversity in hexaploid and tetraploid wheat and their interspecific hybrids. Photosynth. Res. 20:105-118.

Comstock, R.E., and R.H. moll. 1963. Genotypic- environment interactions. p. 164-194. *In* W.D. Hanson and H.F. Robinson (ed.) Statistical genetics and

plant breeding. Pub. 982. Nat'l. Acad. Sci. –Nat'l. Res. Council. Washington, D.C.

Davidson, D.J., and P.M. Chevalier. 1992. Storage and remobilization of water-soluble carbohydrates in stems of spring wheat. Crop Sci. 32: 186-190.

Davidson, J.L., and J.W. Birch. 1978. Response of standard Australian and Mexican wheat to temperature and water stress. Aust. J. Agric. Res. 29:1091-1106.

Deckerd, E.L, R.H. Busch, and K.D. Kofoid. 1985. Physiological aspects of spring wheat improvement. p.45. *In* J. Hasper et al. (ed.) Exploration of physiological and genetics variability to enhanced crop productivity. American Soc. Plant Phys., Madison, WI.

Dhuyvetter, K.C., C.R. Thompson, C.A. Norwood, and A.D. Halvorson. 1996. Economics of dryland cropping systems in the Great Plains: A review. J. Prod. Agric. 9:216-222.

Dubois, D., M. Winzeler, and J. Nosberger. 1990. Fructan accumulation and sucrose: sucrose fructosyltransferase activity in stems of spring wheat genotypes. Crop Sci. 30:315-319.

Evans, L.T., and H.M. Rawson. 1970. Photosynthesis and respiration by the flag leaf and components of the ear during grain development in wheat. Aust. J. Biol. Sci. 23:245-254.

Evans, L.T., I.F. Wardlaw, and R.A. Fischer. 1975. Wheat. p.101-149. *In* L.T. Evans (ed.) Crop physiology: Some case histories. Cambridge University Press, London, UK.

Fehr, W.R. 1987. Principles of cultivars development: Theory and technique. Vol. 1. Macmillan Pub. New York.

Feil, B. 1992. Breeding progress in small grain cereals – A comparison of old and modern cultivars. Plant Breed. 108:1-11.

Fischer, D.B., and R.M. Gifford. 1986. Accumulation and conversion of sugar by developing wheat grains. VI. Gradients along the transport pathway from the peduncle to the endosperm cavity during grain filling. Plant Physiol. 82: 1024-1030.

Fischer, R.A. 1973. The effect of water stress at various stages of development on yield processes in wheat. p. 233-241. *In* R.O. Slatyer (ed.) Plant response to climatic factors. Proc. Uppsala Symp., UNESCO, Paris.

Fischer, R.A. 1984. Wheat. p. 129-153. *In* W. H. Smith and S.J. Banta (ed.) Symposium on potential productivity of field crops under different environments. IRRI, Los Baños, The Phillipines.

Fischer, R.A. 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. J. Agri. Sci. 100:447-461.

Fischer, R.A., and Y.M. Stockman. 1986. Increased kernel number in Norin 10-derived dwarf wheat: Evaluation of a cause. Aust. J. Plant Physiol. 13:767-784.

Frederick, J.R. 1997. Winter wheat leaf photosynthesis, stomatal conductance, and leaf N concentration during reproductive development. Crop Sci. 37:1819-1826.

Frederick, J.R., and J.J. Camberatto. 1995. Water and nitrogen on wheat in southeastern costal plain. I. Grain yield and kernel traits. Agron. J. 87: 521-526.

Frederick, J.R., and P.H. Bauer. 1999. Physiological and numerical components of wheat yield. p. 45 –65. *In* E.H. Sattore and G.A. Slafer (ed.) Wheat: Ecology and physiology of yield determination. Haworth Press Inc., Binghamton, NY.

Gallagher, J.N., P.V. Biscoe, and B. Hunter. 1976. Effects of drought on grain growth. Nature 264:541-542.

Gallagher, J.N., P.V. Biscoe, and R.K. Scott. 1975a. Barley and its environment. IV. Growth and development in relation to yield. J. Appl. Biol. 13:563-583.

Gallagher, J.N., P.V. Biscoe, and R.K. Scott. 1975b. Barley and its environment. V. Stability of grain weight. J. Appl. Biol. 12:319-336.

Gardner, J.S., W.M. Hess, and E.J. Trione. 1985. Development of a young wheat spike: ASEM study of Chinese spring wheat. Am. J. Bot. 72:548- 559.

Gebeyehou, G., D.R. Knott and R.J. Baker. 1982. Rate and duration of grain filling in durum wheat cultivars. Crop Sci. 22:337-340.

Gomez, K.A., and A.A. Gomez. 1984. Statistical procedures for agricultural research. 2nd ed. John Wiley and sons, New York.

Graybosch, R.A., C.J. Peterson, D.R. Shelton, and P.S. Baenziger. 1996. Genotypic and environmental modification of wheat flour protein composition in relation to end-use quality. Crop Sci. 36: 296-300.

Hale, M.G., and D.M. Orcutt. 1987. The physiology of plants under stress. John Wiley & Sons, Inc., New York, NY.

Haley, S.D., and J.S. Quick. 1993. Early-generation selection for chemical desiccation tolerance in winter wheat. Crop Sci. 33:1217-1223.

Haley, S.D., and J.S. Quick. 1998. Methodology for evaluation of chemical desiccation tolerance in winter wheat. Cereal Res. Commun. 26:73-79.

Hallauer, A.R., and J.B. Miranda Filho. 1981. Quantitative genetics in maize breeding. Iowa State Univ. Press, Ames, IA.

Haun, J.R. 1973. Visual quantification of wheat development. Agron. J. 65:116-119.

Hawker, J.S., and C.F.Jenner. 1993. High temperature affects the activity of enzymes in the committed pathway of starch synthesis in developing wheat endosperm. Aust. J. Plant Physiol. 20: 197-209.

Hay, R.K.M., and A.J. Walker. 1987. An introduction to the physiology of crop yield. John Wiley & Sons, Inc., New York, NY.

Hendrix, J.E. 1995. Assimilate transport and partitioning. p. 357-385. *In* M. Pessarakli (ed.) Handbook of plant and crop physiology. Marcel Dekker Inc., New York, NY.

Hendrix, J.E., J.C. Linden, D.H. Smith, C.W. Ross, and I.K. Park. 1986. Relationship of pre-anthesis fructan metabolism to grain numbers in winter wheat (*Triticum aestivum)*. Aust. J. Plant Physiol. 13:391-398.

Hossian, A.B.S, R.G. Sears, T.S. Cox, and G.M. Paulsen. 1990. Desiccation tolerance and its relationship to assimilate partioning in winter wheat. Crop Sci. 30:622-627.

Hsiao, T.C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24:519-570.

Hunt, L.A. 1978. Stem weight changes during grain filling in wheat from diverse sources. 5th international wheat genetics symposium. New Delhi, India. p. 923-929.

Jenner, C.F., and A.J. Rathjen. 1975. Factors regulating the accumulation of starch in ripening wheat grain. Aust. J. Plant Physiol. 2:311-322.

Johnson, R.C., B.F. Carver, D.W. Mornhinweg, H. Kebede, D.M. Ferris, and A.L. Rayburn 1978. Photosynthetic variation in *Triticum dicoccoides* accessions: physiology and genetics. Plant Physiol. Biochem. 26:439.

Johnson, V.A., J.W. Schmidt, and W. Mekasha. 1966. Comparison of yield components and agronomic characteristics of four winter wheat varieties differing in plant height. Agron. J. 58:438-441.

Kiniry,J.R. 1993. Nonstructural carbohydrate utilization by wheat shaded during grain growth. Agron. J. 85:844-849.

Kirby, E.J.M. 1988. Analysis of leaf, stem and ear growth in wheat from terminal sipkelet stage to anthesis. Field Crops Res. 25:25-264.

Kirby, E.J.M., and M.W. Perry. 1987. Leaf emergence rate of wheat in a Mediterranean environment. Aus.J. Agric. Res. 38:455-464.

Kobata T., J.A. Palta, and N.C. Turner. 1992. Rate of development of postanthesis water deficits and grain filling of spring wheat. Crop Sci. 32:1230-1242.

Kronstad, W.E., and D.N. Moss 1989. Requirements of plant breeders from physiologists to increase selection efficiency. *In* E. Acevedo, A.P. Conesa, P.Monneveux, and J.P. Srivastava (ed.) Proc. Int. Symp. on Physiology-Breeding of Winter Cereals for Stressed Mediterranean Environments. Montpellier, France.

Kuhbauch, W., and U.Thome. 1989. Nonstructural carbohydrates of wheat stem as influenced by sink-source manipulations. J. Plant Physiol. 134:243-250.

Large, E.C. 1954. Growth stages in cereals: Illustration of the Feekes scale. Plant Pathol. 3:128-129.

Ledent, J.F., and D.N. Moss. 1979. Relation of morphological characters and shoot yield in wheat. Crop Sci. 19:445-451.

Loss, S.P., and K.H.M. Siddique. 1994. Morphological and physiological traits associated with wheat yield increases in Mediterranean environments. Agronomy. 52:229-276.

Mahalakshmi, V., F.P.Bidinger, K.P. Rao, and S.P.Wani. 1994. Use of the senescing agent potassium iodide to simulate water deficit during flowering and grain filling in pearl millet. Field Crop Res. 36:103-111.

Martinez-Carrasco, R., and G.N. Thorne. 1979. Physiological factor limiting grain size in wheat. J. Exp. Bot. 30:669-679.

Masle, J. 1985. Competition among tillers in winter wheat: consequences for growth and development of the crop. p. 33-54. *In W.* Day and R.K.Atkin (ed.) Wheat growth and modeling. Plenum Press, New York, NY.

McCaig, T.N., and J.M. Clarke. 1982. Seasonal changes in nonstructural carbohydrate levels of wheat and oats grown in a semiarid environment. Crop Sci. 22:963-970.

McKenzie, H. 1972. Adverse influence of awns on yield of wheat. Can. J. Plant Sci. 52:81-87.

Miralles, D.J., and G. A. Slafer. 1999. Wheat Development. p. 13-43. *In E.H.* Sattore and G.A.Slafer (ed.) Wheat: ecology and physiology of yield determination. Haworth press Inc., Binghamton, NY.

Miralles, D.J., and G.A. Slafer. 1995. Yield, biomass, and yield components in dwarf, semidwarf and tall isogeneic lines of spring wheat under recommended and late sowing dates. Plant Breed. 114:392- 396.

Nicolas, M.E., and N.C. Turner. 1993. Use of chemical desiccants and senescing agents to select wheat lines maintaining stable grain size during post-anthesis drought. Field Crops Res. 31:155-171.

Nicolas, M.E., R.M. Gleadow, and M.J. Dalling . 1984. Effects of drought and high temperature on grain growth in wheat. Aust. J. Plant Physiol. 11:17-22.

Palta, J.A., T. Kobata, N.C. Turner, and I.R. Fillery. 1994. Remobilization of carbon and nitrogen in wheat as influenced by postanthesis water deficits. Crop Sci. 34:118-124.

Perry, M.W., and M.F. D'Antuono. 1989. Yield improvement and associated characteristics of some Australian spring wheat cultivars introduced between 1860 and 1982. Aust. J. Agric. Res. 40:457-472.

Pheloung, P.C., and K.H.M. Siddique. 1991. Contribution of stem dry matter to grain yield in wheat cultivars. Aust. J. Plant Physiol. 18:53-64.

Puckridge, D. W. 1969. Photosynthesis of wheat under field conditions. II. Effect of defoliation on the carbon dioxide uptake of the community. Aust. J. Agric. Res. 20:623-634.

Rawson, H.M., and C.M. Donald. 1969. The absorption and distribution of nitrogen, after floret initiation in wheat. Aust. J. Agric. Res. 20:799-808.

Rawson, H.M., and G. Hofstra. 1969. Translocation and remobilization of ^{14}C assimilated at different stages by leaf of the wheat plant. Aust. J. Biol. Sci. 22: 321-331.

Rawson, H.M., and L.T. Evans. 1970. The pattern of grain growth within the ear of wheat. Aust. J. Biol. Sci. 23:753-764.

Rawson, H.M., and L.T. Evans. 1971. The contribution of stem reserves to grain development in a range of wheat cultivars of different height. Aust. J. Agric. Res. 22:851-861.

Rawson, H.M., J.H. Hindmarsh, R.A. Fischer, and Y.M. Stockman. 1983. Changes in leaf photosynthesis with plant ontogeny and relationships with yield per ear in wheat cultivars and 120 progeny. Aust. J. Plant Physiol. 10:503-514.

Richards, R.A. 1996a. Defining selection criteria to improve yield under drought. Plant Growth Reg. 20:157-166.

Richards, R.A. 1996b. Increasing yield potential in wheat – source and sink limitations. p. 134-149. *In* M. P. Reynolds, S. Rajaram, and A. McNab (ed.) Increasing Yield Potential in Wheat: Breaking the Barriers. CIMMYT, Mexico, DF.

Santibanez, F. 1994. Crop requirements – Temperate crops. p. 174-188. *In* J. Griffith (ed.) Handbook of Agricultural Meteorology. Oxford University Press, Oxford, UK.

SAS Institute. 1988. SAS/ STAT user's guide: release 6:03 SAS Inst. Cary, NC.

Savin, R., and G.A. Slafer. 1991. Shading effects on the yield of an Argentinean wheat cultivar. J. Agric. Sci. 116:1-7.

Savin, R., P.J. Stone, and M.E. Nicolas. 1996. Responses of grain growth and malting quality of barely to short periods of high temperature in field studies using portable chambers. Aust. J. Agric. Res. 47:465-477.

Schuler, S.F., R.K. Bacon and E.E. Gbur.1994. Kernel and spike character influence on test weight of soft red winter wheat. Crop Sci. 34: 1309-1313.

Shanahan, J.F., D.H. Smith, and J.R. Welsh. 1984. An analysis of postanthesis sink limited winter wheat grain yield under various environments. Agron. J. 76:611-614.

Sibony, M., and M.J. Pinthus. 1988. Floret initiation and development in spring wheat (*Triticum aestivum L.).* Ann. Bot. 62:473- 479.

Siddique, K.H.M., E.J.M. Kirby, and M.W. Perry. 1989. Ear- to-stem ratio in old and modern wheats; relationship with improvement in number of grains per ear and yield. Field Crops Res.21:59-78.

Simmons, S.R. 1987. Growth, development, and physiology. p. 77-113. *In* E.G. Heyne (ed.) Wheat and wheat improvement 2nd ed. Agron. Monogr. 13. ASA, CSSA, and SSSA, Madison, WI.

Simmons, S.R., and R.K. Crookston. 1979. Rate and duration of growth of kernels formed at specific florets in spikelets of spring wheat. Crop Sci. 19:690-693.

Simmons, S.R., R.K. Crookston, and J.E. Kurle. 1982. Growth of spring wheat kernels as influenced by reduced kernel number per spikes and defoliation. Crop Sci. 22:983-988.

Singh, B.K., and C.F. Jenner 1982. Association between concentrations of organic nutrients in the grain, endosperm cell number and grain dry weight within the ear of wheat. Aust. J. Plant Physiol. 9:83-95.

Slafer, G.A., and F.H. Andrade. 1991. Changes in physiological attributes of the dry matter economy of bread wheat *(Triticum aestivum)* through genetic improvement of grain yield potential at different regions of the world. Euphytica 58:37-49.

Slafer, G.A., and F.H. Andrade. 1993. Physiological attributes related to the generation of grain yield wheat cultivars released at different eras. Field Crops Res. 31:351.

Slafer, G.A., D.F. Calderini, D.J. Miralles, and M.F. Dreccer. 1994b. Pre-anthesis shading effects on the number of grains of three bread wheat cultivars of different potential number of grains. Field crops Res. 36:31-39.

Slafer, G.A., E.H. Satorre, and F.H. Andrade. 1994a. Increases in grain yield in bread wheat from breeding and associated physiological change. p. 1-68. *In* G.A. Slafer (ed.) Genetic Improvement of Field Crops. Marcel Dekker Inc., New York, NY.

Slafer, G.A., F.H. Andrade, and E.H. Sattorre. 1990. Genetic improvement effects on pre-anthesis physiological attributes related to wheat grain yield. Field Crops Res. 23:255.

Slafer, G.A., J.L. Araus, and R.A. Richards. 1999. Physiological traits that increase the yield potential of wheat . p. 379- 415. *In* E.H. Satore and G.A. Slafer (ed.) Wheat: Ecology and physiology of yield determination. Haworth Press Inc., Binghamton, NY.

Slayter, R.O. 1969. Physiological significant of internal water relations to crop yield. p.53-83. *In* Easting, J. D. (ed.) Physiological aspects of crop yields. ASA, CSSA, Madison, WI.

Sofield, I., L.T. Evans, M.G. Cook, and I.F. Wardlaw. 1977. Factors influencing the rate and duration of grain filling in wheat. Aust. J. Plant Physiol. 4:785-797.

Spiertz, J.H.J., B.A. Tennhag, and L.J.P. Kupens. 1971. Relation between green area duration and grain yield in some varieties of spring wheat. Neth. J. Agric. Sci. 19:211-222.

Stapper, M., and R.A. Fischer. 1990. Genotype, sowing date and planting spacing influence on high-yielding irrigated wheat in Southern New South Wales. I. Phasic development, canopy growth and spike production. Aust.J. Agric. Res. 41:997- 1019.

Syme, J.R. 1974. Leaf appearance rate and associated characters in some Mexican and Australian wheats. Aust.J. Agric. Res. 25:1-7.

Teare, L.D., J.W. Sij, R.P. Waldern, and S.M. Goltz. 1972. Comparative data on the rate of photosynthesis, respiration and transpiration of different organs in awned and awnless isogeneic lines of wheat. Can. J. Plant Sci. 52:965-971.

Thorne, G.N., and D.W. Wood. 1987. Effects of radiation and temperature on tiller survival, grain number and grain yield in winter wheat. Ann. Bot. 59:413-426.

Turner, N.C. 1986. Adaptation to water deficits: A changing perspective. Aust. J. Plant Physiol., 13:175-190.

Turner, N.C., and M.E. Nicolas. 1987. Drought resistance of wheat for light-textured soils in a Mediterranean climate. p. 203-215. *In* J. P. Srivastava et al. (ed.) Drought tolerance in winter cereals. John Wiley & Sons, Ltd., New York, NY.

Turner, N.C., M.E. Nicolas, K.T. Hubick, and G.D. Farquhar. 1989. Evaluation of traits for the improvement of water use efficiency and harvest index. p. 177-190. *In* F.W.G. Baker (ed.) Drought resistance in cereals. CAB International, Wallingford, Oxon, UK.

Waddington, S.R., J.K. Ransom, M. Osmaszai, and D.A. Saunders. 1986. Improvement in the yield potential of bread wheat adapted to northwest Mexico. Crop Sci. 26:698.

Waddington, S.R., P.M. Cartwright, and P.C., Wall. 1983. A quantitative scale of spike initial and pistil development in barely and wheat. Ann. Bot. 51:119-130.

Wardlaw, I.F. 1967. The effect of water stress on translocation in relation to photosynthesis and growth. I. Effect during grain development in wheat. Aust. J. Biol. Sci. 20:25-39.

Wardlaw, I.F. 1968. The control and pattern of movement of carbohydrates in plants. Bot. Rev. 34:79-105.

Wardlaw, I.F., and H.K. Porter. 1967. The redistribution of stem sugars in wheat during grain development. Aust.J. Biol. Sci. 20:309-318.

Wardlaw, I.F., and L. Moncur. 1976. Source, sink and hormonal control of translocation in wheat. Planta. 128:93-100.

Yemm, E.W., and A.J. Willis. 1954. The estimation of carbohydrates in plant extracts by anthrone. Biochemical J. 57:508-514.

Youssefian, S., E.J.M. Kirby, and M.D. Gale. 1992. Pleiotropic effects of the G.A. insensitive *Rht* dwarfing gene in wheat. 2. Effects on leaf stem and ear growth. Field Crops Res. 28:191-210.

Zadoks, J.C., T.T. Chang, and C.F. Konzak. 1974. A decimal code for the growth stages of cereals. Weed Res. 14:415-421.