Evaluating a Conceptual Model for Drought Tolerance

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Summary

Wheat yields are reduced by 50–90% of their irrigated potential by drought on at least 60 million ha in the developing world. CIMMYT's wheat program is attempting to further improve drought tolerance by introgressing stress adaptive traits into empirically selected drought tolerant germplasm. Our current conceptual model for drought encompasses high expression of the following traits: seed size, coleoptile length, early ground cover, pre-anthesis biomass, stem reserves/remobilization, spike photosynthesis, stomatal conductance, osmotic adjustment, accumulation of abscisic acid (ABA), heat tolerance, leaf anatomical traits (waxiness, pubescence, rolling, thickness), high tiller survival, and stay-green. CIMMYT's germplasm collection is being screened for high expression of these traits. The traits will be tested systematically either in recombinant inbred lines, near isogenics, or synthetic hexaploids. Molecular markers will be developed for those traits showing genetic gains to selection.

Introduction

At least 60 million ha of wheat is grown in marginal rainfed environments in developing countries. National average yields range from 0.8 to 1.5 t/ha, approximately 10 to 50% of their theoretical irrigated potential (Morris et al. 1991). Rainfall distribution patterns vary considerably among locations and years, and additional stresses may include heat and cold stress, soil micro-element deficiency or toxicity, and a range of biotic stresses. Physiological assessment of drought tolerance characteristics in the field is therefore a complex task. Research at CIMMYT using a line-source gradient to create different intensities of drought stress demonstrated a linear relationship between grain yield and water application (Sayre et al. 1995). This suggests that wheat is relatively drought hardy, unlike maize for example, which may fail completely if the anthesis-silking interval is delayed beyond a critical threshold due to drought (Bolaños and Edmeades 1993). Breeding for drought tolerance in wheat, therefore, should focus more on improving overall radiation use efficiency under stress rather than reproductive stages of growth and partitioning. This conclusion is backed by recent studies with *Rht* isolines in which the shorter growth habit normally associated with better partitioning to yield was of no benefit under drought (Singh, personal communication).

CIMMYT's breeding work for moisture-stressed environments has been largely empirical to date (Pfeiffer and Trethowan 1999), but recent emphasis on breeding for marginal environments has increased the focus on dry environments, and a multidisciplinary effort has been initiated to improve drought tolerance. The main inputs from a physiological point of view will be (i) to develop conceptual models of trait combinations which may enhance drought tolerance; (ii) identify sources of those traits among current breeders materials and germplasm bank accessions including landraces; (iii) evaluate genetic gains associated with specific traits or trait combinations when introgressed into different adapted backgrounds; (iv) pre-screen diploid and tetraploid genotypes for use in development of synthetic wheat lines so as to increase the probability of favorable traits being expressed in hexaploid and tetraploid combinations; (v) evaluate traits in genetically mapped populations to identify molecular markers for drought tolerance genes; and (vi) establish stress treatments for functional genomics studies and identify traits for crop improvement based on genetic dissection.

For the purposes of this workshop, the focus will be on a drought environment broadly characterized as follows: average yield 1.0–2.0 t/ha (approximately 25% of irrigated yield potential), moisture deficit starting after approximately 30 days (jointing) and gradually intensifying until maturity, possible heat stress (air temperature > 30°C) during grain filling. This environment is reasonably representative of most rainfed wheat growing regions in Asia and North Africa. Nonetheless, within this broad region, significant differences occur between sites for factors such as rainfall distribution pattern, soil water holding capacity, agronomic practices etc., and breeding objectives need to take account of this variability.

A Conceptual Model for Drought Tolerance

Many anatomical, physiological and biochemical traits are mentioned in the literature as being drought adaptive (Blum 1988; Loss and Siddique 1994; Richards 1996). This model will include those which are currently considered of most potential value to the environment described (Figure 1), bearing in mind that not all traits are appropriate for all drought environments. The development of molecular probes for marker-assisted screening of these traits would be an important objective, assuming their use is more efficient at identifying superior genotypes than conventional screening approaches.

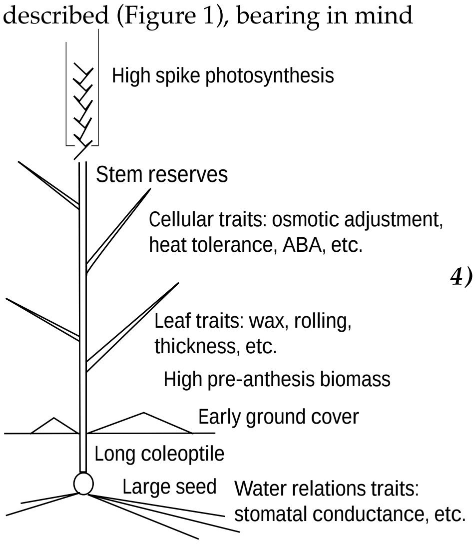

Figure 1. Conceptual model of drought tolerant wheat plant.

1) ***Large seed size.*** Helps emergence, early ground cover, and initial biomass.
2) ***Long coleoptiles.*** For emergence from deep sowing (Radford 1987). This is practiced to help seedlings reach the receding moisture profile, and to avoid high soil surface temperatures which inhibit germination.
3) ***Early ground cover.*** Thinner, wider leaves (i.e., with a relatively low specific leaf weight) and a more prostrate growth habit help to increase ground cover, thus conserving soil moisture and potentially increasing radiation use efficiency. (Richards 1996). This trait would be more important in the Mediterranean type of drought environment where rain may occur during the early part of the cycle. It would be less useful in regions where the crop grows exclusively on stored soil moisture where dust mulching is practiced, or where residue retention is practiced to avoid evaporation from the soil surface.
4) ***High pre-anthesis biomass.*** Potential for vigorous growth prior to heading provides the opportunity to take advantage of relatively good growing temperatures and moisture availability earlier in the cycle. Up to 40% of available water may be lost by evaporation directly from the soil in Mediterranean types of environments (Loss and Siddique 1994), so high early ground cover and biomass production may permit a more efficient use of soil water. Although most drought studies show that high water use efficiency (WUE) is not associated with better performance (e.g., Sayre et al. 1995), ideally early biomass should be achieved with maximal water use efficiency to improve water availability during grain filling. Recent work in Australia (Richards, personal communication) indicate an advantage of high WUE genotypes under severe drought conditions.
5) ***Good capacity for stem reserves and remobilization.*** Stored fructans can contribute substantially to grain filling, especially when canopy photosynthesis is inhibited by drought (Rawson and Evans 1971). Traits that may contribute include long and thick stem internodes, with extra storage tissue perhaps in the form of solid stems. In studies where crosses where made between lines contrasting in the solid stem trait, the solid-stem progeny contained more soluble carbohydrate per unit of stem length, though total stem carbohydrate was unaffected due to narrower and shorter stems (Ford et al. 1979).
6) ***High spike photosynthetic capacity***. Spikes have higher WUE than leaves and have been shown to contribute up to 40% of total carbon fixation under moisture stress (Evans et al. 1972). Awns contribute substantially to spike photosynthesis and longer awns are a possible selection criterion.

While gas exchange measurement of spikes is time consuming and difficult to standardize, chlorophyll fluorescence should be considered as a more rapid means of screening for spike photosynthetic capacity under stress (P. Horton, personal communication). The trait could be measured at any time after heading.

7) ***High RLWC/Gs/CTD during grain filling to indicate ability to extract water.*** A root system that can extract whatever water is available in the soil profile is clearly drought adaptive (Hurd 1968), but difficult to measure. Traits affected by the water relations of the plant, such as relative leaf water content (RLWC) measured pre-dawn, stomatal conductance (Gs), or canopy temperature depression (CTD), during the day, and C_{13} discrimination or ash content of grain or other tissues, can give indications of water extraction patterns.
8) ***Osmotic adjustment.*** (Morgan and Condon 1986). Adjustment will help maintain leaf metabolism and root growth at relatively low leaf water potentials by maintaining turgor pressure in the cells. Some research suggests that the trait can be assayed relatively easily by measuring coleoptile growth rate of seedlings in polyethylene glycol (PEG) solution.
9) ***Accumulation of ABA***. The benefit of ABA accumulation under drought has been demonstrated (Innes et al. 1984). It appears to pre-adapt plants to stress by reducing stomatal conductance, rates of cell division, organ size, and increasing development rate. However, high ABA can also result in sterility problems since high ABA levels may abort developing florets.
10) ***Heat Tolerance.*** The contribution of heat tolerance to performance under moisture stress needs to be quantified, but it is relatively easy to screen for (Reynolds et al. 1998).
11) ***Leaf anatomy: waxiness, pubescence, rolling, thickness, posture*** (Richards 1996). These traits decrease radiation load to the leaf surface. Benefits include a lower evapotranspiration rate and reduced risk of irreversible photo-inhibition. However, they may also be associated with reduce radiation use efficiency, which would reduce yield under more favorable conditions.
12) ***High tiller survival.*** Comparison of old and new varieties have shown that under drought older varieties over-produce tillers many of which fail to set grain while modern drought tolerant lines produce fewer tillers most of which survive (Siddique and Loss 1994).
13) ***Stay-green.*** The trait may indicate the presence of drought avoidance mechanisms, but probably does not contribute to yield per se if there is no water left in the soil profile by the end of the cycle to support leaf gas exchange. It may be detrimental if it indicates lack of ability to remobilize stem reserves (Blum 1998). However, research in sorghum has indicated that stay-green is associated with higher leaf chlorophyll content at all stages of development and both were associated with improved yield and transpiration efficiency under drought (Borrel et al. 2000)

Identification of Sources with High Expression of Drought-adaptive Traits

Germplasm bank accessions, for example land race collections from heat or drought stressed regions such as Iran and Mexico, are being systematically screened for potentially valuable traits. Sources have been identified with high chlorophyll at heading (Hede et al. 1999), high leaf conductance (Villhelmsen et al. 1999), high pubescence (Trethowan et al. 1998), peduncle volume, stay-green, and heat tolerance. Searches are currently under way for long awns, high osmotic adjustment, and biomass under drought and high temperature stress.

Pre-screening Diploid and Tetraploid Genotypes for Making Synthetic Wheat

Dicoccums, durum land races and diploid genome donors are being systematically screened for a number of the traits described above. Lines showing drought adaptive traits can be used to generate synthetic wheat.

Evaluation of Genetic Gains for Traits Introgressed into Drought-tolerant Backgrounds

So far studies have only been accomplished in recombinant inbred lines (RILs). The main focus has been measurement of canopy temperature depression (CTD) to indicate differences in stomatal conductance of water. CTD showed a highly significant association with yield under drought when measured pre-anthesis (Figure 2), suggesting an advantage from higher growth rates pre-anthesis. When measured during grain filling, CTD also showed a good association with final yield (Figure 3). Genetic variation for awn length, stem thickness and solid stem were estimated in two populations of RILs. Average awn length ranged from 5.5 to 9 mm, average stem thickness of the main tiller (3 cm below the spike) ranged from 1.6 mm to 2.6 mm, but no relationship between yield and these traits was revealed. The solid stem trait was estimated on a visual basis and rated from 1 to 5 where 5 was completely solid. The trait appeared to be facultative in as much as under irrigation all lines scored 1, while under stress there was a full range of expression. However, the trait was negatively associated with yield in two populations of RILs.

Evaluate Traits in Genetically Mapped Populations to Identify Molecular Markers

To date, the only mapped material available at CIMMYT has been the ITMI population (International Triticale Mapping Initiative). The lines are the progeny of a wide cross between a synthetic line (having good drought tolerance) and Opata-M85 (a relatively drought susceptible semi-dwarf). This material has been evaluated for yield, yield loss (relative to lines without stress), and CTD under both drought (Figure 3) and heat. Yield loss under drought ranged from 50% to 95% of well-watered controls, and there was a significant association between yield under drought and yield under heat stress (Figure 4), indicating the value of heat tolerance as a drought adaptive trait. When QTL analysis has been realized, it should be possible to detect QTL markers associated with yield stability under drought. In addition, QTLs for CTD can be compared under drought, heat, and well watered conditions to determine genomic regions which are associated with higher CTD specifically under stressed conditions. Since CTD is determined by stomatal conductance, if there is such a unique linkage of QTLs associated with high CTD under drought, they would be expected to be associated with traits permitting better water relations in these conditions. A new population has also been developed for stress work between two semidwarf lines (Seri-M82 and Babax) which contrast in performance under drought, but whose progeny are quite similar in height and phenology and thus very amenable to physiological studies.

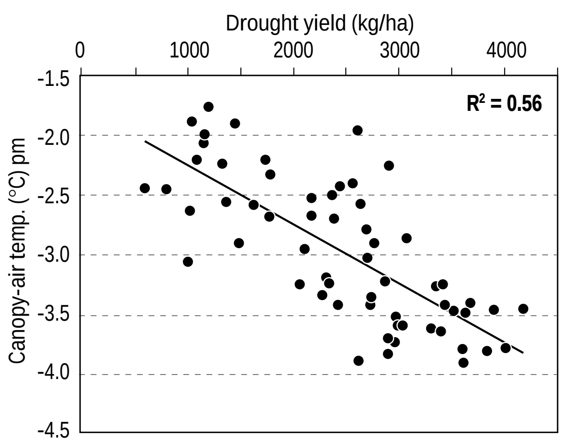

Figure 2. Association of canopy temperature depression measured pre-heading with yield under drought of recombinant inbred lines from the cross Babax/Lucero-Mexicano, Obregon,1998-99.

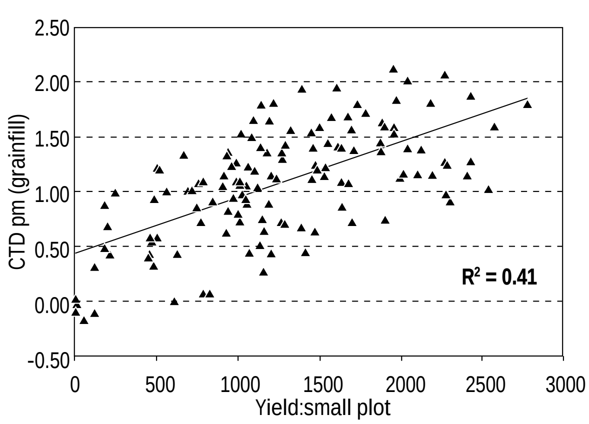

Figure 3. Association of canopy temperature depression measured during grain filling with yield under drought of recombinant inbred lines of the ITMI population (Synthetic/Opata-M85) Obregon 1997-98.

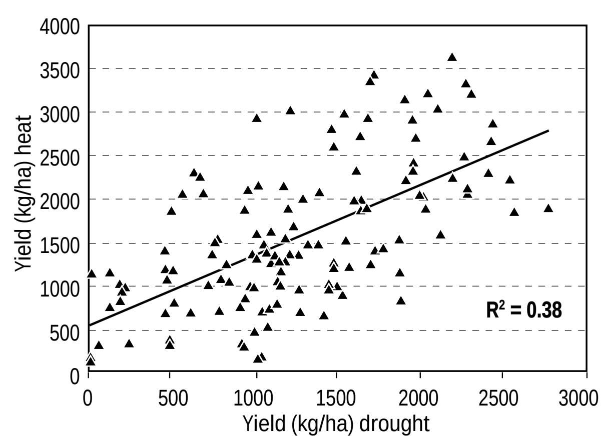

Figure 4. Association of yield under drought with yield under heat stress for recombinant inbred lines of the ITMI population (Synthetic/Opata-M85) Obregon 1997-98.

This will be mapped and evaluated for a number of drought adaptive traits in subsequent cycles.

Establish Stress Treatments for Functional Genomics Studies and Identify Traits for Genetic Improvement Based on Genetic Dissection

With the advent of DNA chip technology or micro-arrays (Brownstein et al. 1998), the relative importance of different genes involved in drought tolerance could be determined. The technique involves extracting RNA from plant tissue and generating labelled cDNA or cRNA probes that are hybridized with the microarrays. The microarrays are scanned to determine which genes were turned on in the tissue sample. Since so many genes are involved, a very large amount of information is generated for each sample. Therefore, it will be important to use physiological understanding to chose the most appropriate plant organs, stages of phenology and stress conditions to focus the research, in order to discover candidate genes for crop improvement. Once the microarray data has been interpreted, it should indicate the types of physiological traits that need to be exploited in terms of introgression of new sources of genetic diversity to improve drought tolerance.

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