**Drought resistance in wild emmer wheat: Physiology, ecology, and genetics**

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**ABSTRACT**

Drought is the main environmental stress limiting crop productivity and yield stability worldwide. Improving drought resistance of crop plants is considered a sustainable and economically viable solution to increasing agricultural productivity under diminishing water availability. The implementation of this solution requires wide explorations of potential genetic resources and in-depth understanding of their adaptive mechanisms and responses to water deficit. In this minireview we summarize the physiological, ecological, and genetic aspects of drought resistance in wild emmer wheat [Triticum turgidum ssp. dicoccoides (Körn.) Thell.] and discuss their implications on wheat improvement.

A comprehensive survey of wild emmer wheat populations, collected across the aridity gradient in Israel, revealed wide genetic diversity for drought responses, with a considerable number of wild accessions exhibiting an advantage over durum wheat cultivars. A variety of adaptive traits associated with improved performances under water-limited conditions, including phenology and water use efficiency, were identified in wild emmer wheat. The greatest allelic diversity, as well as the highest drought resistance capacity, were observed in wild emmer populations from intermediate aridity levels exposed to the greatest climatic fluctuations. It is concluded that the wild emmer wheat gene pool harbors a rich allelic repertoire for various morpho-physiological traits conferring drought resistance that are potentially useful for wheat improvement. An ongoing mapping study revealed numerous quantitative trait loci (QTLs) underlying the observed drought resistance that may serve as a starting point for introgression and marker-assisted breeding.

**Keywords:** earliness, genetic diversity, Triticum turgidum ssp. dicoccoides, productivity, water-use efficiency, wheat breeding, drought resistance

**INTRODUCTION**

Inadequate water availability, often combined with high temperature stress, is the main abiotic factor limiting crop productivity in many parts of the world (Kramer, 1980; Boyer, 1982; Araus et al., 2002). Water availability for agriculture is becoming limited alongside a projected rise in food demand for the expanding world population. Moreover, climate-change scenarios predict an increased aridity in many regions of the world. The development of novel cultivars with more efficient water-use and greater drought resistance capacity is considered a sustainable and economically viable solution to this problem (Bacon, 2004; Condon et al., 2004). The implementation of this solution requires wide explorations of potential genetic resources and in-depth understanding of the ecophysiological and genetic adaptive mechanisms and responses to water deficiency. The dissection of plant responses to drought stress will...
provide a solid foundation for genetic improvement of crop productivity under arid conditions (Blum, 1988).

The genetic diversity of wild progenitors of crop plants is much wider compared with their descendant crop plants (e.g., Harlan, 1992; Tanksley and McCouch, 1997). The major reasons for this almost universal phenomenon are the genetic bottlenecks associated with plant domestication (e.g., founder effect; Ladizinsky, 1998) and subsequent selection in man-made agroecosystems (e.g., Abbo et al., 2003). As a result of the narrowing of genetic diversity, modern crop plants have become more vulnerable to environmental stresses. Therefore, a major objective of modern breeding is to identify, in the wild ancestors of crop plants, valuable “left behind” alleles and introduce them into cultivated crops (Aaronsohn, 1910; Tanksley and McCouch, 1997; Gur and Zamir, 2004; Uauy et al., 2006). Furthermore, the comparison between the wild species and their domesticated counterparts offers an indispensable opportunity for understanding the physiological and genetic basis of crop adaptations (Evans, 1993 and references therein).

Wild emmer wheat [Triticum turgidum ssp. dicoccoides (Körn.) Thell.] is the allo-tetraploid (2n = 4x = 28; genome BBA) progenitor of cultivated wheats (Feldman, 2001). It is fully compatible with the tetraploid (2n = 4x = 28; BBA) durum wheat [T. turgidum ssp. durum (Desf.) MacKey] and can be crossed with the hexaploid (2n = 6x = 42; BBAADD) bread wheat (T. aestivum L.) (Feldman and Sears, 1981). Wild emmer is distributed throughout the Near Eastern “Fertile Crescent”, across a variety of ecological conditions, from hot and dry (with as little as 230 mm annual rainfall) to cool and humid (with over 1300 mm) habitats (Harlan and Zohary, 1966). Hence, the wild emmer genepool offers a rich allelic repertoire required for improvement of numerous economically important traits such as protein and mineral contents in grain, disease resistance, herbicide resistance, and salinity tolerance (e.g., Feldman and Sears, 1981; Nevo et al., 2002 and references therein). However, until recently very little has been published on drought responses in wild emmer wheat.

In this minireview, we summarize the ecological, physiological, and genetic aspects of drought resistance in wild emmer wheat and discuss their implications on wheat improvement.

**ECOPHYSIOLOGY OF BIOMASS PRODUCTION AND PARTITIONING**

Since the dawn of Near Eastern agriculture in the Neolithic period, about 10,000 years ago (Lev-Yadun et al., 2000), and up to the present, wheat has remained an outstanding crop in terms of cultivated area and importance as a major food source (Evans, 1998 and references therein). Nowadays, wheat provides about one-fifth of the calories consumed by humans, with 620 million tons produced annually worldwide (FAOstat, 2006). To reach the forecasted demand for wheat in the coming decades, global production will need to increase by 1.6 to 2.6% annually (Braun et al., 1998). Future increase in wheat production is strongly dependent on higher yields rather than on augmenting the harvested area (Araus et al., 2003). This scenario is further complicated when considering that as much as 50% of the wheat production area is regularly affected by drought (Pfeiffer et al., 2005).

Fischer and Wood (1978) reported that yield under drought was positively associated with total dry matter (DM) at maturity in durum wheat, bread wheat, and barley. Out of 39 wild emmer accessions, 33% exhibited a smaller rate of injury (greater resistance) to seedling growth under osmotic stress, as compared with cultivated wheat controls (Blum et al., 1983). Nevo et al. (1984) noted genotype × environment interaction in productivity of wild emmer accessions tested under xeric and mesic environments in Israel. Peleg et al. (2005) reported that about 80% out of 110 wild emmer accessions produced, under water-limited field conditions, greater total DM than domesticated durum lines (Fig. 1B). Selected lines (drought resistant and susceptible), tested in larger plots in a subsequent year, further confirmed these results (Peleg et al., 2008b). Higher biomass accumulation under limited water conditions was also noted in comparison of several Aegilops spp. and wild Triticum spp. vs. durum wheat lines (Rafi et al., 1992).

The improvement of harvest index (HI; the ratio of reproductive biomass to total biomass) played a major role in the genetic improvement of wheat yields over the past 50 years, following the green revolution (Evans, 1993). Several studies suggested that greater assimilate allocation to the spike plays a major role in grain yield (Sayre et al., 1997; Araus et al., 2002). Although wild emmer was never subjected to direct selection for yield or HI, about 30% out of 110 wild emmer accessions produced greater spike DM (representing reproductive biomass) under water deficiency than the cultivated durum lines (Fig. 1A; Peleg et al., 2005).

Under stable environments, either stressful or non-stressful, high productivity is one of the most important factors required to maximize grain yield, whereas under fluctuating environments high stability is also required. A considerable number of wild emmer accessions exhibited higher stability (low drought susceptibility indices; Fischer and Maurer, 1978) for both spike DM and total biomass.
DM (Fig. 1) as compared with durum wheat cultivars, reflecting greater drought adaptations in the former. The combination of high productivity with low stress susceptibility would be most desirable. Seven out of the 25 wild emmer wheat populations examined (namely: Achihood, Yehudiyya, Gitit, Givat Koach, Kokhav Hayarden, Ma’ale Merav, and Mt. Gilboa) combined high productivity under water-limited conditions with higher stability (Peleg et al., 2005). These populations offer the greatest potential for improvement of drought adaptation in wheat.

**TRADEOFF BETWEEN FLOWERING TIME AND BIOMASS PRODUCTION**

Flowering time is a major trait that coordinates plants’ life cycle with local environmental conditions in both wild and cultivated annual plant species. Depending on abiotic (water, photoperiod, temperature, nutrients) and biotic (competition, pollinators, herbivores) conditions, different flowering patterns have been adopted by various wild plant species (Roux et al., 2006). While under optimal growing conditions, late flowering leads to a longer vegetative growth period that promotes the accumulation and allocation of resources to seed production, early flowering (drought escape) improves fitness in environments with a short or unpredictable growing season. The tradeoff between resource accumulation and drought escape is of primary importance for crop yield and quality, and the identification of variations associated with flowering time is a key component in improving plant adaptation to different latitudes and cropping seasons.

Under Mediterranean conditions, water deficit and high temperature during the grain-filling period (i.e., terminal drought) are very common, causing dramatic reductions in crop yields (Loss and Siddique, 1994). Terminal drought escape through early reproduction has been a very successful breeding strategy for Mediterranean environments (Araus et al., 2004 and references therein). Furthermore, empirical selection (i.e., for yield improvement) has been a key component in improving plant adaptation to different latitudes and cropping seasons.

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*Fig. 1. Frequency distribution of 110 wild emmer wheat accessions for the spike dry matter (A) and total dry matter (B) under well-watered (650 mm) and water-limited (250 mm) irrigation regimes, as well as in terms of drought susceptibility index (S; Fischer and Maurer, 1978). Arrows above the histograms indicate the values of three durum wheat cultivars (d = 580D, i = Inbar, and s = Svevo). Data adapted from Peleg et al. (2005).*
The term carbon isotope discrimination (\( \Delta \)) expressing the difference between \( \delta^{13}C \) of the plant and that of the air [\( \Delta = (\delta^{13}C_{\text{air}} - \delta^{13}C_{\text{plant}})/(1 + \delta^{13}C_{\text{plant}}/1000) \)] is used alternatively to \( \delta^{13}C \). Since \( \delta^{13}C_{\text{plant}}/1000 \) is a negligibly small value and \( \delta^{13}C_{\text{air}} \) is fairly stable in open plant canopies, \( \Delta \) is considered inversely related to \( \delta^{13}C_{\text{plant}} \). The term \( \delta^{13}C \) is used throughout this review, also when citing publications where \( \Delta \) was originally used.

WATER-USE EFFICIENCY AND ITS ASSOCIATION WITH PRODUCTIVITY

Water-use efficiency (WUE), defined in agronomic terms as the ratio between yield production and water consumption or in physiological terms as the ratio between photosynthesis and transpiration rates, is an important character determining crop performance under limited water availability (Condon and Hall, 1997). Stable carbon isotope ratio (\( ^{13}C/^{12}C \), expressed in differential notation as \( \delta^{13}C \)) in plant tissues is a well-established indirect measure of WUE (Farquhar and Richards, 1984). While variation in \( \delta^{13}C \) (and WUE) and its relationship with productivity has been extensively documented in cultivated wheats (Araus et al., 2004), very little is known about this aspect in wild emmer wheat. Under a water-limited environment, wild emmer exhibited a wide genetic diversity for \( \delta^{13}C \) (ca. 3.5‰) as well as an advantage (ca. 1.2‰) over durum wheat cultivars (Peleg et al., 2005 and unpublished data). For a given vapor pressure deficit (VPD), an increase of 1‰ variation in \( \delta^{13}C \) may represent ca. 15% in variation in WUE (Hubick and Farquhar, 1989; Morgan et al., 1993). Moreover, most wild emmer accessions show a considerably higher phenotypic plasticity for \( \delta^{13}C \) (increased WUE under water deficiency) as compared with the cultivated durum controls (Peleg et al., 2005). Likewise, increased \( \delta^{13}C \) in response to drought conditions has also been found in wild barley populations (Handley et al., 1994) and durum wheat genotypes (Merah et al., 2001). The ability of an individual organism to alter its form of function in response to environmental changes is believed to be an advantageous evolutionary response to environmental heterogeneity (Bradshaw, 1965). These finding suggest that adaptive mechanisms of WUE in cultivated wheat could be improved by introgression from its wild relatives.

The greatest difficulty of using \( \delta^{13}C \) in breeding programs for drought environment is the high level of inconsistency observed in the relationship between \( \delta^{13}C \) and biomass production in wheat (and other C₃ cereals) (Condon et al., 2004; Blum, 2005). High WUE (and \( \delta^{13}C \)) can be achieved either through increased photosynthetic rate or reduced stomatal conductance (Morgan and LeCain, 1991). At the instantaneous physiological level only the former strategy would increase productivity; however, at the whole plant level the latter strategy may be critical for survival and productivity under drought conditions. The challenge in research of WUE is to achieve “higher photosynthetic rate at lower stomatal conductance” (Tambussi et al., 2007). Recently Rebetzke et al. (2002) showed that bread wheat lines selected for high \( \delta^{13}C \) (higher WUE) exhibited greater aerial biomass and grain yield than lines selected for low \( \delta^{13}C \), most remarkably under water-limited environments.

In wild emmer wheat, \( \delta^{13}C \) was positively correlated with total DM under both well-watered and water-limited conditions; however, it was not correlated with spike DM (Peleg et al., 2005). The complex relationships between WUE and productivity were further dissected by principal component analysis (PCA) of various drought-related responses in wild emmer wheat (Fig. 3). High \( \delta^{13}C \) under water-limited conditions (on the upper half
of Fig. 3) was associated either with high productivity under water deficiency and low drought susceptibility (on the upper right part) or low productivity and high susceptibility (on the upper left part). These contrasting responses seem to arise from different photosynthetic capacities. A selected accession from the high productivity high WUE group (#12–3) exhibited much greater photosynthetic rate under ambient [CO\textsubscript{2}] as compared with an accession (#24–39) from the low-productivity high WUE group (Avneri et al., 2007). Therefore, wild emmer wheat accessions from the high-productivity high WUE group could serve as donors in future breeding programs.

**GENETIC DIVERSITY ASSOCIATED WITH NATURAL ARIDITY GRADIENT**

Environmental stress gradients are ubiquitous evolutionary forces, shaping biological diversity at all levels of organization (e.g., Darwin, 1859). Native stands of wild emmer wheat thrive across wide ecological amplitude in diverse natural habitats differing from one another in a large number of variables, such as macro- and micro-climate, topography, substrate (soil type, bedrock), vegetative community, grazing, and other disturbances (e.g., Harlan and Zohary, 1966; Feldman and Sears, 1981). Such local differentiation may enhance plant populations to evolve local ecological adaptations that provide an advantage under the prevailing conditions.

Twenty-five wild emmer wheat populations collected across an aridity gradient in Israel have been clustered into six groups based on their microsatellite marker genetic similarity (Peleg et al., 2008a). Several groups were comprised of populations collected in ecologically similar but geographically remote habitats, emphasizing the importance of environmental conditions in shaping the populations’ genetic structure. Likewise, drought responses in wild emmer wheat were found to be associated with ecogeographical variables of the populations’ collection sites (Peleg et al., 2005).

Wide genetic diversity, both between and within populations of wild emmer wheat, has been reported for various phenotypic characteristics (e.g., Nevo et al., 2002) including drought responses (Blum et al., 1983; Peleg et al., 2005). This is further supported by wide microsatellite marker allelic diversity between and within populations (e.g., Fahima et al., 2002; Peleg et al., 2008a, 2008c). The high level of within-population allelic diversity (>50%) indicates that the wild emmer populations, although collected across small habitats, are comprised of large numbers of considerably different multi-locus genotypes. The within-population allelic diversity exhibited a unimodal association with several environmental factors, indicating that the highest diversity evolved in populations that originated from habitats with intermediate environmental stress (e.g., rainfall 350–550 mm/year) (Peleg et al., 2008a). These habitats are subjected to wide inter- and intra-annual environmental variabilities that impose fluctuating selection pressure and lead to higher genetic diversity. Moreover, six out of the seven populations that combined high productivity and stability across water availability treatments (see above) originated from such intermediate environments. Surprisingly, wild emmer accessions from the most xeric habitats (<300 mm rainfall per annum) exhibited relatively low drought resistance capacity (Peleg et al., 2005) as well as low microsatellite marker allelic diversity (Peleg et al., 2008a). It is hypothesized that these populations exploit a drought escape strategy either on an annual (producing in rainy years) or spatial (growing in wet micro-niches) scale and thus are able to survive in such harsh environments.

**FACING THE FUTURE: WILD EMMER AS POTENTIAL SOURCE FOR WHEAT IMPROVEMENTS**

During a long evolutionary history across a range of environmental conditions in the Near Eastern Fertile Crescent, wild emmer wheat has accumulated a wealth of genetic diversity and adaptations to multiple biotic and abiotic stress conditions (Feldman and Sears, 1981;
Nevo et al., 2002). Shortly after discovering the wild emmer wheat, A. Aaronsohn envisioned that: “…the cultivation of wheat may be revolutionized by the utilization of these wild forms .... to produce races better adapted to semi-arid regions...” (Aaronsohn, 1910). The materialization of this vision, yet unachieved, has recently become more feasible with novel scientific tools and an urgent necessity in light of the eroded genetic diversity. During the early and mid 20th century, a lack of genetic and cytological knowledge discouraged the utilization of wild emmer germplasm in breeding programs (Feldman and Millet, 2001). Nearly half a century later, wild emmer wheat regained new interest as a source for disease resistance (Nevo et al., 2002) and high protein contents (Avivi, 1979), which have led to breeding programs and gene discovery (Uauy et al., 2006). In the 1980s, alongside the increasing awareness to maintain food security under diminishing water availability, wild emmer was evaluated for drought resistance in two studies (Blum et al., 1983; Nevo et al., 1984), which were not continued. Our recent comprehensive survey of wild emmer wheat populations from across an aridity gradient in Israel revealed a wide phenotypic and allelic diversity for drought response (Peleg et al., 2005, 2008a,b,c), demonstrating the potential of the wild gene pool for wheat improvement.

Global climatic changes towards increased aridity and direct anthropogenic modification of the environment accelerate the extinction of wild emmer wheat’s natural habitats. The greatest allelic diversity and drought resistance capacity were found in wild emmer populations from intermediate-stress habitats; hence, high priority should be given to conservation of these populations. The recent designation of the Amiad (Eastern Galilee) nature reserve for in-situ conservation of wild emmer wheat (Kaplan, 2007) is an important step towards this direction. The large proportion of the genetic variation residing within populations, as well as the various drought resistance strategies identified within the wild emmer gene pool, call for further exploration of promising populations and for studying their adaptive mechanisms to establish the essential basis for wheat improvement.

An on-going genetic dissection of drought-related traits, through quantitative trait loci (QTL) analysis of a recombinant inbreed line population derived from a cross between wild emmer and durum wheat, sheds light on drought-adaptive mechanisms (Peleg et al., in preparation). A total of 73 QTLs were associated with productivity and drought-related morpho-physiological traits, with numerous wild emmer alleles superior to durum wheat alleles. Associations between QTLs for various traits suggest that several mechanisms are involved in adaptation to drought stress. These results may serve as a starting point for introgression of promising QTLs into elite cultivated materials via marker-assisted selection.

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