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FERTILE CRESCENT REGION AS SOURCE OF DROUGHT TOLERANCE AT EARLY STAGE OF PLANT GROWTH OF WILD BARLEY (*HORDEUM VULGARE* L. SSP. *SPONTANEUM)*

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Abstract

Drought is one of the most important types of abiotic stress that affects stability and amount of yield. This study was conducted to screen for drought tolerance at early seedling stages for 318 ecogeographically diverse wild barley (*Hordeum vulgare* L. spp. *spontaneum*) diversity collection (WBDC). Considerable variation was observed for all the seedling characters examined. Seedling growth was significantly reduced by 17% polyethyleneglycol-induced drought stress with significant variation among accessions. Shoot length was the most sensitive trait, however, root-shoot length ratio increased under osmotic stress. Correlation studies indicated that the root length was the most important trait, followed by shoot length and root-shoot length ratio. Principal components analysis (PCA) was performed and the first two principal components (PC) explained 78.3% of the variation present in the WBDC with PC1 (50.1%) associated with shoot length and seedling length. PC2 (28.1%) was related with root length and root-shoot length ratio. PCA showed that accessions from the Fertile Crescent particularly from Jordan and Israel showed high drought tolerance than other geographical regions at the early seedling stage. The accessions WBDC009 (Jordan), WBDC075 (Libya), WBDC211 (Uzbekistan), WBDC242 (Jordan), WBDC254 (Jordan) and WBDC289 (Israel) exhibited the highest drought tolerance index, indicating high level of drought tolerance. Consequently, these accessions showed tolerance to drought at the early seedling stage and are considered to be good sources of drought tolerance for cultivated barley improvement.

Introduction

Among the different abiotic stresses, drought is most complex and devastating on a global scale (Pennisi, 2008). The sustainable and economically viable solution for increasing crop productivity in arid and semiarid zones is genetic improvement (Blum, 1988). In cereal crops which provide the major carbohydrate staples for humans, even intermittent water stress at critical stages may result in considerable yield reduction (Ludlow & Muchow, 1990). It is often discussed and emphasized that crop genetic improvement lies in exploiting the gene pools of the wild relatives of the crop plant (Nevo *et al.,* 2002).

Wild barley (*Hordeum vulgare* L. ssp. *spontaneum* (C. Koch) Thell), the progenitor of cultivated barley, is widespread in the Near East Fertile Crescent (Zohary & Hopf,

1988) and harbors a large genetic variation (Gunaskera *et al*., 1994). It occupies diverse habitats ranging from high rainfall regions to deserts (Volis *et al*., 2002a). The wide ecological range of wild barley habitat differs in water availability, temperature, soil type, altitude, and vegetation generating a high potential of adaptive diversity to abiotic stresses. Wild barley is a valuable source of new genes for breeding. These include resistance to powdery mildew (Dreiseitl & Dinoor, 2004), resistance to multiple diseases (Yun *et al.,* 2005), earliness (Li *et al.,* 2005), biomass under drought (Lu *et al.,* 1999), plant height under drought (Baum *et al.,* 2003), drought tolerance (Volis *et al.,* 1998; Ivandic *et al.,* 2000; Robinson *et al.,* 2000; Baum *et al.,* 2003), and cold tolerance (Grossi *et al.,* 1998).

Water shortage is the major constraint affecting cereal production in the Mediterranean Basin. The climate of this region is characterized by erratic and unpredictable precipitations. Although drought may occur at any stage of cereal development in these areas, climatic frequency studies have identified two major periods when drought is most likely to occur (Loss & Siddique, 1994). The first occurs in autumn during the period from sowing to tillering. The second major drought period coincides with the grain-filling phase. Impacts of terminal water stress on cereals have been thoroughly investigated, while studies of early season drought are lacking. An early season drought may affect considerably yields through the limitation of tiller survival rate and number of kernels produced (Hafid *et al.,* 1998a).

Selection of tolerant cultivars has been considered as an economic and efficient means to improve drought tolerance (Chloupek & Rod, 1992; Turner, 1997). A better understanding of mechanisms of adaptation to water deficit and maintenance of growth, development and productivity during stress periods would help the drought-tolerance breeding (Chloupek & Rod, 1992). Nevertheless, drought tolerance is a complex trait resulting from the contribution of numerous factors. Among the several putative characters, water status parameters (Merah, 2001, Szira *et al.*, 2008) carbon isotope discrimination (Merah, 2001), roots and shoot characters (Hafid *et al.,* 1998b; Dhanda *et al.,* 2004; Szira *et al.,* 2008), root-shoot partitioning (Thornley, 1998; Dhanda *et al.,* 2004), early growth vigour (Hafid *et al.,* 1998b; Dhanda *et al.,* 2004) are interesting traits for drought-tolerance evaluation. Szira *et al.*, (2008) suggest that the drought stress induced by polyethyleneglycol (PEG) at germination stage is quick, simple, cheap and provides many reproducible data and adequate to pre-select large number of genotypes at early growth stages.

The development of extensive root system contributes to differences among cereal cultivars for drought tolerance (Fukai & Cooper, 1995; Turner, 1997). Genotypic variability has been found in many species for shoot and root characters (Wahbi & Gregory, 1989, Tischler *et al.,* 1989), and its significance for drought tolerance improvement discussed (Chloupek & Rod 1992; Turner, 1997; Fukai & Cooper, 1995). An appreciable genotypic diversity for shoot and root growth at early stages was reported in barley under favorable conditions or under other abiotic stress (Wahbi & Gregory, 1989; Saito *et al.,* 1999; Malik *et al.,* 2002). There is limited insight into morphological traits of shoot and seminal roots in wild barley at early plant growth stage under drought in a large population, although this species is mainly cultivated without irrigation in arid and semi-arid regions. Early water stress seems to damage the number of tillers and the number of grains per ear (Guedira *et al.,* 1997, Volkmar, 1997), which strongly reduces yield production in cereals (Turner, 1997). The most studied traits were volume, length and number of seminal roots as well as the root-to-shoot dry matters ratio. It was reported that the number of seminal roots is slightly or not affected by water deficit (Guedira, 1997; Volkmar, 1997). However, root and shoot lengths were considered as efficient characters to evaluate genotype response to water stress at seedling stage (Guedira, 1997; Volkmar, 1997; Dhanda *et al.,* 2004; Szira *et al.,* 2008).

In the absence of any information on morphological traits of shoots and seminal roots in large wild barley population under water-deficit conditions, the major objectives of this study was to identify drought tolerant wild barley accessions at early seedling stage and to assess the extent and structure of genetic diversity in an ecogeographically diverse collection of wild barley.

Materials and Methods

Plant materials: Three hundred and eighteen wild barley accessions were assembled for the Wild Barley Diversity Collection (WBDC) by Dr. Jan Valkoun (Barley Curator, ICARDA, Aleppo, Syria) and B. Steffenson (University of Minnesota, USA) (Steffenson *et al.,* 2007). The WBDC accessions were selected based on various ecogeographic characters (e.g. longitude/latitude, elevation, high/low temperature, rainfall, soil type) and were from 19 different countries, mostly in the Fertile Crescent (243/315 or 77.1%), but also from Central Asia (50/315 or 15.7%), North Africa (12/315 or 3.8%), and the Caucasus region (10/315 or 3.1%) (Roy *et al.,* 2010).

Dormancy break: The wild barley accessions were sown and grown to maturity in a vinyl house at the experimental farm at Chonbuk National University in Jeonju, Korea in 2009. Seeds were harvested and stored at 4°C until analysis. Then, seeds of all 318 accessions were stored at 37°C for one month.

Screening of seedling characters: The 318 wild barley accessions were screened for tolerance to drought stress at the early seedling stage. Ten seeds of uniform size were weighted and surface-sterilized with 3 % (w/v) Sodium hypochlorite for 10 min and then washed thoroughly with deionized water. Seeds were transferred to sterile Petri dishes (100 mm in diameter) containing two layers of Whatman filter paper and were moistened with 10 mL distilled water (control) or 17% (w/v) PEG 6000 (Merck, Darmstadt, Germany) solution. Petri dishes were placed in a growth chamber with a temperature of 20 ±2°C and a 12 h light/12 h dark photoperiod at 60% relative humidity with two replicates. Petri dishes were tightly sealed with parafilm (O_2 permeable) to prevent evaporation of water, thus minimizing changes in the concentration of solutions. Preliminary experiments with ten accessions grown with PEG concentrations of 12 to 24%, found that 17% PEG gave the best discrimination between accessions (K. Tyagi *et al.,* unpublished results). Ten days after incubation, 5 uniform and representative seedlings were selected; observation and measurement were performed on the following traits: seedling length (mm), shoot length (mm), root length (mm), seminal root number and root-shoot length ratio.

Statistical analysis: The drought tolerance index (TI) (Szira *et al.,* 2008) was calculated as the ratio of data derived from the stress (S) and control treatment (C) for each traits e.g., for SL TI = SL S/SL C.

Principal component analyses (PCA) were performed using the seedling traits. The mean trait values obtained from data set relating to stress performance was created by calculating TI for individual traits were used for PCA. Principal components were then derived from this TI data set to identify stress tolerance accessions i. e., accessions that were least affected by the drought-stress treatment.

PCA was also conducting to see any relationship among the geographical origin (Fertile Crescent, Central Asia, North Africa and Caucasus Region) and within Fertile Crescent (Syria, Israel, Turkey, Jordan, Lebanon, Iran and Iraq) for drought tolerance in wild barley. Analysis of variance and PCA were performed using SPSS (SPSS Inc., Chicago, Illinois, USA).

Results

Effect of osmotic stress on seedling traits: The wild barley accessions revealed significant difference ($p<0.001$) for all the traits investigated in this experiment, indicating a high level of genetic variability (Table 1). Drought caused significant ($P< 0.001$) reduction in seedling length, shoot length, root length, seminal root number and root-shoot length ratio (Tables 1 and 2). Mean squares due to accessions and drought stress interaction were significant ($p<0.001$) for all traits, indicating traits performance of accessions in different growing conditions (Table 1). Shoot length was highly reduced in response to drought stress. At 17% PEG, seedling length was reduced by 29%, shoot length by 48%, root length by 5%, seminal root number by 23%, and root-shoot ratio by 7% compared with the control, respectively (Table 2).

Relationship among traits under control and stress conditions: Correlations were analyzed between the control and drought stress conditions for the traits (Table 3). Root length was positively and significantly correlated with root-shoot length ratio ($r = 0.90$, $p<0.001$), seedling length ($r = 0.89$, $p<0.001$) and moderately correlated with shoot length ($r = .031$, $p<0.001$) under the control condition. But under the drought stress condition root lenght was moderately correlated with root-shoot length ratio ($r = 0.53$, $p<0.001$). This indicated that shoot length was reduced more than the root length under the osmotic stress condition. Root-shoot length ratio showed weak relationships with all the traits except root length ($r = 0.90$, $p<0.001$) and seedling length ($r = 0.63$, $p<0.001$) under control condition, but under drought stress it was negatively correlated with shoot length ($r = -0.38$, $p<0.001$). Seminal root number was not highly correlated with any traits (Table 3). Seedling length positively and significantly correlated with all the traits except seminal root number under the control condition, but under the drought stress it showed weak correlation with root-shoot length ratio ($r = 0.16$, $p<0.001$).

Principal component analysis: Principal components analysis (PCA) was performed and the first two principal components explained 78.3% of the variation present in the WBDC with PC1 (50.1%) associated with shoot length and seedling length. PC2 (28.1%) was associated with root length and root-shoot length ratio (Table 4). Accessions WBDC009 (Jordan), WBDC075 (Libya), WBDC211 (Uzbekistan), WBDC242 (Jordan), WBDC254 (Jordan) and WBDC289 (Israel) showed the highest drought tolerance among accessions on the basis of all traits combined (Fig. 1). PCA analysis showed that Fertile Crescent has high drought tolerance accessions than the other geographical regions (Fig. 2). The Jordan and Israel has more drought tolerance accessions within Fertile Crescent regions than the other countries in wild barley (Fig. 3).

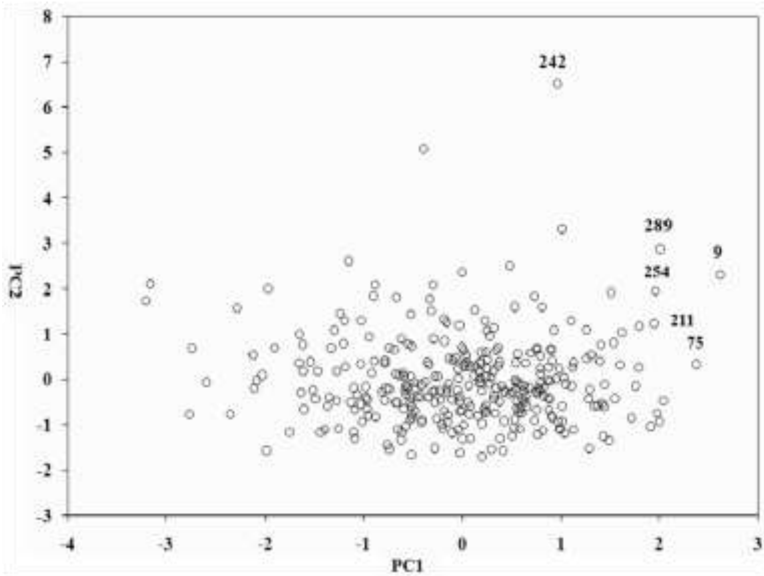

Fig. 1. Principal component analysis of seedling drought tolerance traits in the Wild Barley Diversity Collection. Axes are the two principle components, PC1 and PC2. Key to outlying accessions 9=WBDC009; 75=WBDC075; 211= WBDC211; 242=WBDC242; 254=BDC254 and 289=WBDC289.

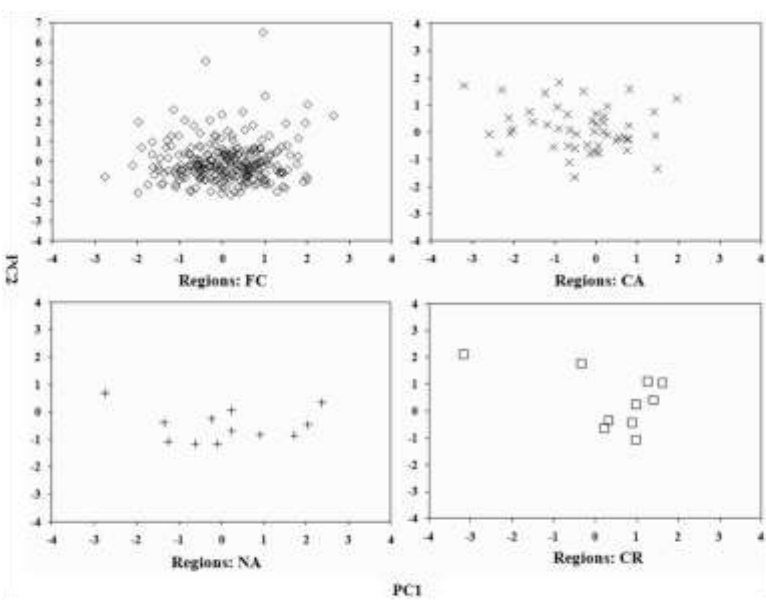

Fig. 2. Principal component analysis of seedling drought tolerance traits with respect to geographical origins of accessions from the Wild Barley Diversity Collection (Fertile Crescent, FC; Central Asia, CA; North Africa, NA; and Caucasus region, CR). Axes are the two principle components, PC1 and PC2.

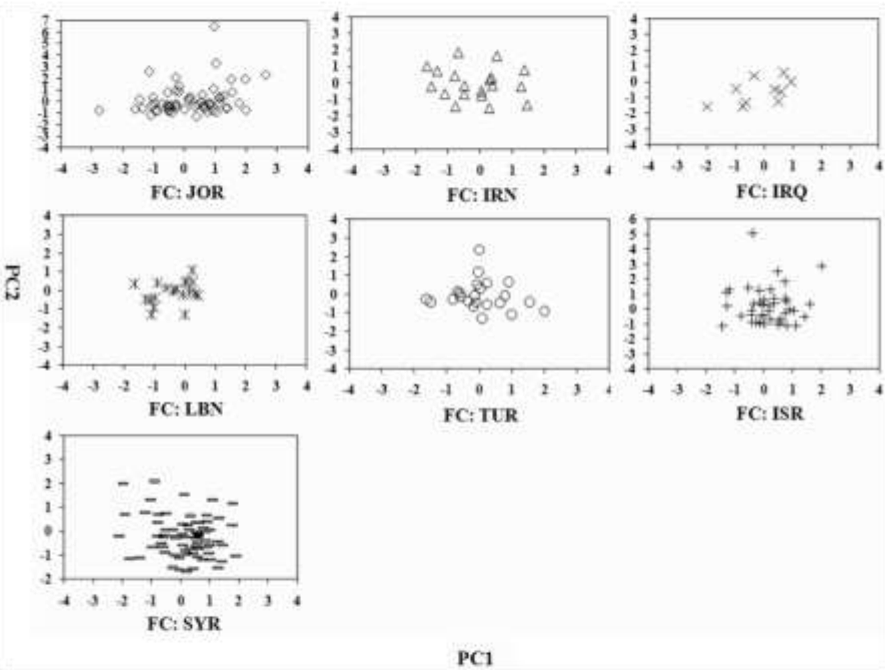

Fig. 3. Principal component analysis of seedling drought tolerance traits of accessions from the Fertile Crescent (Syria, SYR; Israel, ISR; Turkey, TUR; Jordan, JOR; Lebanon, LBN; Iran, IRN and Iraq, IRQ). Axes are the two principle components, PC1and PC2.

Table 1. Mean squares from analysis of variance (ANOVA) for seedling traits of 318 wild barley accessions under 0 (control) and 17% PEG stress level at early stage of plant growth.

Traits	Accessions (317 d. f.)	Drought levels (1 d. f.)	Accessions x Drought (317 d. f.)	Error (5723 d. f.)
Seedling length	22562***	6374404***	5558***	296
Shoot length	4981***	5616866***	917***	97
Root length	10703.3***	24012.6***	3558.6***	134.90
Seminal root number	7.65***	1282.5***	0.92***	0.17
Root-shoot length ratio	1.25***	524.2***	0.56***	0.03

d. f., degree of freedom, *** significant at $p \leq 0.001$

Table 2. Effect of drought stress imposed by osmotic adjustment on seedling traits of 318 wild barley accessions.

Traits	Environment	Minimum	Maximum	% decrease by drought stress compared with control	Mean	SD	CV
Seedling length (mm)	Control	110.00	355.00	29.0	215.55	41.42	19.21
	Stress	43.00	315.00		152.24	40.25	26.44
Shoot length (mm)	Control	65.00	195.00	48.0	124.85	19.44	15.57
	Stress	12.00	135.00		65.41	19.59	29.95
Root length (mm)	Control	15.00	195.00	5.0	80.70	31.00	38.42
	Stress	10.00	175.00		76.82	26.53	34.53
Seminal root number	Control	2.00	7.00	23.0	3.86	0.79	20.52
	Stress	2.00	5.00		2.96	0.72	24.50
Root-shoot length ratio	Control	0.13	1.71	7.0	0.64	0.24	37.07
	Stress	0.23	4.67		1.22	0.43	35.27

SD: Standard deviation; CV: Coefficient of variation

Table 3. Correlation coefficients among seedling traits under control and osmotic stress condition in the Wild Barley Diversity Collection at early plant growth stage.

Traits	Environment	Root length	Root-shoot length ratio	Shoot length	Seminal root number
Root-shoot length ratio	control	0.90***			
	stress	0.53***			
Shoot length	control	0.31***	-0.08***		
	stress	0.51***	-0.38***		
Seminal root number	control	0.10***	-0.00	0.26***	
	stress	0.04***	-0.07***	0.14***	
Seedling length	control	0.89***	0.63***	0.70***	0.20***
	stress	0.90***	0.16***	0.82***	0.10***

*** Statistically significant at $p \leq 0.001$

Table 4. Principal component analysis of drought tolerance in Wild Barley Diversity Collection.

Component contribution variable	1st	2nd
Seedling length (mm)	0.87	0.45
Shoot length (mm)	0.97	-0.20
Root length (mm)	0.49	0.85
Seminal root number	0.00	0.09
Root-shoot length ratio	0.07	0.98
Total variance explained (%)	50.13	28.17
Accumulated variance (%)	50.13	78.30

Discussion

Drought has a large influence on plant growth during germination, vegetative and the reproductive stages. At each stage, it acts as a constraint to crop productivity. However, drought occurring at the early developmental stages has been largely neglected in studies of drought tolerance. Significant differences were observed between water treatments studied (Table 1). Similar differences were reported in several species on roots and early seedling traits (Narayan, 1991; Dhanda *et al*., 2004; Szira *et al*., 2008). Most of these works have also found significant interactions between water stress and genotype, which mirrored differential response patterns to increasing water stress. Similar results were obtained in our study (Table 1). Thus, the variation of accessions over the environments could provide scope of breeding for seedling traits, along with yield and its components, under drought stress conditions. A large variation was observed here for all seedling traits studied (Table 2). Similar results were found for shoot and root traits (Volkmar, 1997; Dhanda *et al*., 2004) in wheat. The few studies performed in barley shoot and roots under osmotic stress (Szira *et al*., 2008) or under favourable conditions (Brown *et al*., 1987; Wahbi & Gregory, 1995) also observed genotypic variability. Our results emphasized the existence of appreciable differences in shoot and root traits in wild barley grown under drought stress conditions (Tables 2). We observed reduction in seedling traits in the drought stress condition (Table 2). Several studies have reported the effect of water stress on shoot and root length in wheat (Hafid *et al*., 1998b; Guedira *et al*., 1997; Volkmar *et* *al*., 1997; Dhanda *et al*., 2004) in oat (Murphy *et al*., 1982), cultivated barley (Szira *et al*., 2008) and wild barley (Lu *et al*., 1999). The mean of root-shoot length ratio, however, increased under drought stress (Table 2). This may be attributable to more inhibition of shoot length than root length under stress. This result was expected and confirmed those reported in several other species (Thornley, 1998; Hafid *et al*., 1998b; Grzesiak *et al*., 1999; Dhanda *et al*., 2004). The possible causes of increased root-shoot length ratio under water stress may be the limited supply of water and nutrients to the shoot and some hormonal messages induced in the roots when they encounter drought stress (Sharp & Davis, 1989). The root-to-shoot ratio increases under water-stress conditions to facilitate water absorption (Nicholas, 1998). The continued growth of roots in drying soil is particularly important to avoid drought (Dhanda *et al*., 1995).

Some accessions showed increase in root length and seedling length under drought stress. It may be due to phenotypic plasticity of these traits under drought stress condition. Volis *et al*., (2002b) observed the phenotypic plasticity in root biomass under water stress condition.

Among the seedling traits root length was the most important trait because the accessions with longer roots under drought stress also showed higher root-shoot length ratio ($r = 0.53$, $p<0.001$), shoot length ($r = 0.51$, $p<0.001$) and seedling length ($r = 0.90$, $p<0.001$). The continued growth of root under stress is particularly important to avoid drought for turgor maintenance by osmotic adjustment (Stephen & Siddique, 1994; Basnyake *et al*., 1996). Hafid *et al*., (1998 a) also reported sufficient intraspecific variation for seedling traits to suggest their use as selection tools for drought resistance in wheat. The use of the germination traits in the osmoticum to predict drought resistance was also tried in the past with inconsistent results (Blum, 1988). Root-shoot length ratio showed weak relationships with other traits under normal conditions, but under osmotic stress it was negatively correlated with shoot length ($r = -0.38$, $p<0.001$). Similar results were found in the previous studies on wheat (Dhanda *et al*., 2004). This indicated that the underground part of the plant plays an important role under drought stress conditions (Siddique *et al.*, 1990; Sharma & Lafever, 1992). In experiments at early growth stages, PEG is widely used as an osmolyte in drought-related tests or comparative studies with NaCl (Kpoghomou *et al*., 1990; Dhanda *et al*., 2004; Liu *et al*., 2007; Szira *et al*., 2008). PEGs with molecular weights of 6000 g mol^{-1} or above are non-penetrating, water-soluble, non-ionic polymers causing osmotic stress in the culture solution (Kramer & Boyer, 1995).

PCA analysis showed that Fertile Crescent (Jordan and Israel) had more drought tolerance accessions than the other regions in wild barley. We identified drought tolerant accession (WBDC289) of wild barley from Israel. ICARDA developed a drought tolerant variety by crossing a landrace with a wild barley line from Israel. This new drought-tolerant variety can produce 50% more grain yield than ordinary barley cultivars under dry land conditions (Ashraf, 2010). Salt tolerant wild barley also were identified from Israel (Nevo *et al*., 1993, Yan *et al*., 2008). Other than Israel we also found the drought tolerance accessions from Jordan (WBDC009, WBDC242 and WBDC254), Libya (WBDC075), and Uzbekistan (WBDC211).

The genetic heterogeneity of wild populations has long been recognized as an important mechanism of adaptation to the environment (Nevo *et al*., 1997). This richness of genetic diversity in wild barley and its occurrence over a wide range of habitats in the region suggest that the genetic resources of wild barley in the Fertile Crescent can be exploited for improvement of cultivated barley (Jana & Pietrzak, 1988). A number of accessions from the Fertile Crescent (especially Jordan and Israel) showing drought tolerance at the seedling stages may be useful for the improvement of drought tolerance in cultivated barley. Exploiting biodiversity for genetic gain is not a new concept. Many major genes from wild relatives have been transferred into the cultivated gene pools of many crops (Hajjar & Hodgkin, 2007).

Conclusion

Shoot length showed greater reduction than other traits and root-shoot length ratio increased under the drought stress. The traits such as seedling length, shoot length, root length, root-shoot length ratio showed considerable variability under the drought stress condition. Correlation studies among these traits revealed that selection for seedling length, shoot length, root length and root-shoot length ratio under drought stress could be instrumental in predicting the drought tolerance of accessions. Correlation studies showed that root length was the most important trait, followed by shoot length and root-shoot length ratio on the basis of their relationship with other traits. The accessions from the Fertile Crescent particularly from Jordan and Israel showed high drought tolerance at the early seedling stage. The accessions WBDC009 (Jordan), WBDC075 (Libya), WBDC211 (Uzbekistan), WBDC242 (Jordan), WBDC254 (Jordan) and WBDC289 (Israel) exhibited the highest TI, indicating high level of drought tolerance at early plant growth stage. Therefore, these wild barley accessions could be considered as drought tolerant and they could be valuable resource in improving drought tolerance of cultivated barley. To exploit the wild barely accessions selected in the present study as gene donors, further studies are necessary to integrate genetic and physiological research. Characterization of genes controlling the physiological characteristics of these wild barley accessions may facilitate the improvement of drought tolerance in cultivated barley. Moreover, more research is required to confirm these results in later growth stages and under field conditions.

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References

Ashraf, M. 2010. Inducing drought tolerance in plants: Recent advances. *Biotechnol. Adv.,* 28: 169-183.

Basnyake, J., M. Cooper, R.G. Henzell and M.M. Ludlow. 1996. Influence of rate of development of water deficit on the expression of maximum osmotic adjustment and desiccation tolerance in three sorghum lines. *Field Crop Res*., 49: 65-76.

Baum, M., S. Grando, G. Backes, A. Jahoor, A. Sabbagh and S Ceccarelli. 2003. QTL for agronomic traits in the Mediterranean environment identified in recombinant inbred lines of the cross ‘Arta’ 9 *H. spontaneum* 41-1. *Theor. Appl. Genet*., 107: 1215-1225.

Brown, B.C., J.D.H. Keatinge, P.J. Gregory and P.J.M. Cooper. 1987. Effects of fertilizers, variety, and location on barley production under rainfed conditions in Northern Syria. I. Root and Shoot growth. *Field Crops Res.,* 16: 53-66.

Blum, A. 1988. *Plant breeding for stress environments*. CRC Press, Boca Raton.

Chloupek, O. and J. Rod. 1992. The root system as a selection criterion. *Plant Breed*. Abstr., 62: 1337-1341.

Dhanda, S.S., R.K. Behl and N. Elbassam. 1995. Breeding wheat genotypes for water deficit environments. *Landbanforschung Volkenrode*, 45: 159-167.

Dhanda, S.S., G.S. Sethi and R.K. Behl. 2004. Indices of drought tolerance in wheat genotypes at early stages of plant growth. *J. Agron. Crop Sci.*, 190: 6-12.

Dreiseitl, A. and A. Dinoor. 2004. Phenotypic diversity of barley mildew resistance sources. *Genet. Resour. Crop Evol.*, 51: 251-257.

Fukai, S. and M. Cooper. 1995. Development of drought-resistant cultivars using physio-morphological traits in rice. *Field Crops Res.*, 40: 67-86.

Grossi, M., E. Giorni, F. Rizza, M.A. Stanca and L. Cattivelli. 1998. Wild and cultivated barleys show differences in the expression pattern of a cold-regulated gene family under different light and temperature conditions. *Plant Mol. Biol.*, 38: 1061-1069.

Grzesiak, S., T. Hura, M.T. Grzesiak and S. Pienskowski. 1999. The impact of limited soil moisture and waterlogging stress conditions on morphophysiological and anatomical roots traits in maize (*Zea mays* L.) hybrids of different drought tolerance. *Acta Physiol. Plant*, 21: 305-315.

Guedira, M., J.P. Shroyer, M.B. Kirkham and G.M. Paulsen. 1997. Wheat coleoptile and root growth and seedling survival after dehydration and rehydration. *Agron. J.*, 89: 822-826.

Gunaskera, D., M. Santakumari, Z. Glinka and G.A. Berkowitz. 1994. Wild and cultivated barley genotypes demonstrate varying ability to acclimate to plant water deficits. *Plant Sci.*, 99: 125-134.

Hafid, R. El., D.H. Smith, M. Karron and K. Samir. 1998a. Physiological responses of spring durum wheat cultivars to early-season drought in a Mediterranean environment. *Ann. Bot.*, 81: 363-370.

Hafid, R. El., D.H. Smith, M. Karrou and K. Samir. 1998b. Root and shoot growth, water use and water use efficiency of spring durum wheat under early-season drought. *Agronomie*, 18: 181-195.

Hajjar, R. and T. Hodgkin 2007. The use of wild relatives in crop improvement: a survey of developments over the last 20 years. *Euphytica*, 156: 1-13.

Ivandic, V., C.A. Hackeet, Z.J. Zhang, J.E. Staub, E. Nevo, W.T.B. Thomas and B.P. Forster. 2000: Phenotypic response of wild barley to experimentally impost water stress. *J. Exp. Bot.*, 51: 2021-2029.

Jana, S. and L. Pietrzak. 1988. Comparative assessment of genetic diversity in wild and primitive cultivated barley in a center of diversity. *Genetics*, 119: 981-990.

Kpoghomou, B.K., V.T. Sapra and C.A. Beyl. 1990. Screening for drought tolerance: soybean germination and its relationship to seedling responses. *J. Agron. Crop Sci.*, 164: 153-159.

Kramer, P.J. and J.S. Boyer. 1995. *Water Relations of Plants and Soils*. Academic press, S an Diego, USA.

Li, J.Z., X.O. Huang, F. Heinrichs and M.W. Ganal. 2005. Analysis of QTLs for yield, yield components, and malting quality in a BC3-DH population of spring barley. *Theor. Appl. Genet.*, 110: 356-363.

Liu, S.H., B.Y. Fu, H.X. Xu, L.H. Zhu, H.Q. Zhai and Z.K. Li. 2007. Cell death in response to osmotic and salt stresses in two rice (*Oryza sativa* L.) ecotypes. *Plant Sci.*, 172: 897-902.

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

Lu, Z., P.M. Neumann, K.Tamar and E. Nevo. 1999. Physiological characterization of drought tolerance in wild barley (*Hordeum spontaneum*) from the Judean Desert. http://wheat.pw.usda.gov/ggpages/bgn/29/a29-09.html

Ludlow, M.M. and R.C. Muchow. 1990. A critical evaluation of traits for improving crop yields in water-limited environments. *Adv. Agron.*, 43: 107-153.

Malik, A.I., T.D. Colmer, H. Lambers, T.L. Setter and M. Shortemeyer. 2002. Short-term waterlogging has long-term effects on the growth and physiology of wheat. *New Phytol.*, 153: 225-236.

Merah, O. 2001. Potential importance of water status traits for durum wheat improvement under Mediterranean conditions. *J. Agric. Sci.,* 137: 139-145.

Murphy, C.F., R.C. Long and L.A. Nelson. 1982. Variability of seedling growth characteristics among oat genotypes. *Crop Sci.,* 22: 1005-1009.

Narayan, D. 1991. Root growth and productivity of wheat cultivars under different soil moisture conditions. *Int. J. Ecol. Environ. Sci.,* 17: 19-26.

Nicholas, S. 1998. Plant resistance to environmental stress. *Curr. Opin. Biotechnol.,* 9: 214-219.

Nevo, E., T. Krugman and A. Beiles. 1993. Genetic resources for salt tolerance in the wild progenitors of wheat (*Triticum dicoccoides*) and barley (*Hordeum spontaneum*) in Israel. *Plant Breed.,* 110: 338-341.

Nevo, E., I. Apelbaum-Elkaher, J. Garty and A. Beiles. 1997. Natural selection causes microscale allozyme diversity in wild barley and a lichen at 'Evolution Canyon', Mt. Carmel, Israel. *Heredity*, 78: 373-382.

Nevo, E., A.B. Korol, A. Beiles and T. Fahima. 2002. Evolution of wild emmer and wheat improvement. Population genetics, genetic resources and genome organization of wheat's progenitor, *Triticum dicoccoides*. Springer, New York.

Pennisi, E. 2008: The blue revolution, drop by drop, gene by gene. *Science*, 320: 171-173.

Robinson, D., I.L.handley, C.M. Scrimgeour, D.C. Gordon, B.P. Forster and R.P. Ellis. 2000. Using stable isotope natural abundance (^{15} N and ^{13} N) to integrate the stress responses of wild barely (*Hordeum spontaneum* C. Koch.) genotypes. *J. Exp. Bot.,* 51: 41-50.

Roy, J.K., K.P. Smith, G.J. Muehlbauer, S. Chao, T.M. Close and B.J. Steffenson. 2010. Association mapping of spot blotch resistance in wild barley. *Mol. Breed.,* 26: 243-256.

Saito, A., Y. Masaoka and K. Sato. 1999. Differential responses of seminal and crown roots among barley cultivars (*Hordeum vulgare* L.) under acid and acid/aluminium stress in hydroponics, Plant & Animal Genome, VII conference, 17–19 January. San Diego, CA, USA. http://intl-pag.com/7/abstracts/pag7653.html.

Sharma, R.C. and N.N. Lafever. 1992. Variability for root traits and their genetic contribution in spring wheat. *Euphytica*, 59: 1-8.

Sharp, R.E. and W.J. Davis. 1989. Regulation of growth and development of plants growing with a restricted supply of water. In: *Plant Under Stress*. (Eds.): H.G. Jones, H.G., T.J. Flowers and M.B. Jones.Cambridge University Press, Cambridge, pp. 71-93.

Siddique, K.H.M., R.K. Belford and D. Tennant. 1990. Root:shoot ratio of old and modern tall and semi-dwarf wheat in a Mediterranean environment. *Aust. J. Agric. Res.,* 40: 473-487.

Stephen, P. L. and K.H.M. Siddique. 1994. Morphological and physiological traits associated with wheat yield increases in Mediterranean environments. *Adv. Agron.,* 46: 229-276.

Steffenson, B.J., P. Olivera, J.K. Roy, Y. Jin, K.P. Smith and G.J. Muehlbauer. 2007. A walk on the wild side: Mining wild wheat and barley collections for rust resistance genes. *Aust. J. Agr. Res.,* 58: 532-544.

Szira, F., A.F. Balint, A. Borner and G. Galiba. 2008. Evaluation of drought-related traits and screening methods at different developmental stages in spring barley. *J. Agron. Crop Sci.,* 194: 334-342.

Thornley, J.M. 1998. Modeling shoot:root relations: the way forward. *Ann. Bot.,* 81: 165-171.

Tischler, C.R., P.W. Voigt and E.C. Holt. 1989. Adventitious root initiation in kleingrass in relation to seedling size and age. *Crop Sci.,* 29: 180-183.

Turner, N.C. 1997. Further progress in crop water relations. *Adv. Agron.,* 58: 293-338.

Volis, S., S. Mendlinger and D. Ward. 2002. Adaptive traits of wild barley of Mediterranean and desert origin. *Oecologia*, 133: 131-138.

Volis, S., S. Mendlinger and D. Ward. 2002. Differentiation in populations of *Hordeum spontaneum* Koch along a gradient of environmental productivity and predictability: plasticity in response to water and nutrient stress. *Biol. J. Lin. Soc.,* 75: 301-312.

Volis, S., S. Mendlinger, L. Olsvig-Whittaker, U.N. Safriel and N. Orlovsky. 1998. Phenotypic variation and stress resistance in core and peripheral populations of *Hordeum spontaneum. Biodiversity and conservation,* 7: 799-813.

Volkmar, K.M. 1997. Water stress nodal roots of wheat: effects on leaf growth. *Aust. J. Plant Physiol.,* 24: 49-56.

Wahbi, A. and P.J. Gregory. 1989. Genotypic differences in root and shoot growth of barley (*Hordeum vulgare*). I. Glasshouse studies of young plants and effects of rooting medium. *Exp. Agric.,* 25: 357-387.

Wahbi, A. and P.J. Gregory. 1995. Growth and development of young roots of barley (*Hordeum vulgare* L.) genotypes. *Ann. Bot.,* 75: 33-539.

Yun, S.J., L. Gyenis, P.M. Hayes, I. Matus, K.P. Smith, B.J. Steffenson and G.J. Muehlbauer. 2005. Quantitative trait loci for multiple disease resistance in wild barley. *Crop Sci.,* 45: 2563-2572.

Yan, J., G. Chen, J. Cheng, E. Nevo and Y. Gutterman. 2008. Phenotypic variation in caryopsis dormancy and seeding salt tolerance in wild barley, *Hordeun spontaneum*, from different habitats in Israel. *Genet. Resour. Crop Evol.,* 55: 995-1005.

Zohary, D and M. Hopf. 1988. *Domestication of plants in the old world*. Clarendon, Oxford Press.

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