Pak. J. Bot., 43(4): 2167-2173, 2011.

DIVERSITY FOR SEEDLING VIGOR IN WILD BARLEY (*HORDEUM VULGARE* L. SUBSP. *SPONTANEUM)* GERMPLASM

KULDEEP TYAGI[1+], MYOUNG RYOUL PARK[1+], HYO JEONG LEE[1], CHONG AE LEE[2], SHAFIQ REHMAN[3], BRIAN STEFFENSON[4], KUI JAE LEE[5], SONG JOONG YUN[1,6*]

[1]*Institute of Agricultural Science and Technology, Chonbuk National University, Jeonju 561-756, Korea;*
[2]*Department of Food Science, Chonbuk National University, Jeonju 561-756, Korea;*
[3]*Department of Botany, Kohat University of Science & Technology (KUST), Kohat 26000, Pakistan;*
[4]*Department of Plant Pathology, University of Minnesota, St. Paul, MN 55108, USA;*
[5]*Division of Biotechnology, Chonbuk National University, Iksan 570-752, Korea;*
[6]*Department of Crop Science, Chonbuk National University, Jeonju 561-756, Korea;*
[*]*Corresponding author, E-mail:* sjyun@chonbuk.ac.kr
[+]KT and MRP contributed equally to this paper

Abstract

Seedling vigor is important for improving stand establishment of barley crops, particularly in arid regions and areas where the soil temperature is low at sowing time. Three hundred and fifteen wild barley accessions from the Wild Barley Diversity Collection (WBDC) were evaluated for nine seedling vigor traits in a polyhouse and growth chamber under hydroponic conditions. The accessions exhibited significant differences for all traits investigated. Traits showing greatest phenotypic variation were seedling visual score, plant height, shoot fresh weight, shoot dry weight and shoot length. Seed weight exhibited the least variation. Seed weight was significantly correlated with visual seedling score and shoot and seedling fresh and dry weight. Correlation analysis showed that the visual seedling score was a reliable method for estimating seedling vigor in wild barley. The first three principal components (PC) explained 82.3% of the variation present in the WBDC with PC1 (54.0%) associated with shoot fresh weight, shoot dry weight, seedling dry weight, seedling fresh weight, shoot length and seedling length. Accessions from the southwest portion of the Fertile Crescent, like WBDC020 (Turkey), WBDC238 (Jordan) and WBDC244 (Jordan) exhibited the highest positive values for most of the plant vigor traits investigated. These wild barley accessions likely carry alleles that will be useful for the improvement of plant vigor traits in cultivated barley.

Introduction

Barley (*Hordeum vulgare* L.) is an important crop often grown in areas with low rainfall where other crops such as wheat fail to grow (Whabi & Gregory, 1989). Barley exhibits some genetic variation in early vigor (Grando & Ceccarelli, 1995); however, due to decades of intensive breeding, the genetic background of cultivated barley is rather narrow. Wild relatives constitute a potential rich source of genetic variation for crop improvement (Feldman & Sears, 1981). Despite the fact that their overall performance is agronomically less desirable, favorable alleles are present in wild relatives (Ellis *et al*., 2000). Wild barley, *Hordeum vulgare* L. ssp. *spontaneum* Koch., is the progenitor of cultivated barley, *H. vulgare* L. and is widespread across the Near East Fertile Crescent (Zohary, 1969). Wild barley is a diploid, predominantly self-pollinated annual that harbors great genetic variation (Gunaskera *et al.*, 1994; Petersen *et al.*, 1994; Volis *et al.*, 2001). The genetic heterogeneity of wild populations has been recognized for its importance in adaptation to the environment (Volis *et al.*, 2002, 2005, 2010). 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 and Central Asia can be exploited for improvement of cultivated barley (Jana & Pietrzak, 1988). The diversity of regional landraces, local cultivars and related species can have a beneficial role in crop improvement (Feuillet *et al*., 2007). 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).

The performance of genotypes at germination, heterotrophic growth, and early autotrophic growth is collectively referred to as seedling vigor and early vigor (Revilla *et al.*, 1999; Hund *et al.*, 2004). Early vigor is considered an essential component of plant development under most environmental conditions (Ludlow & Muchow, 1990). The early growth of seedlings is crucial for their establishment and hence for their eventual success in terms of biomass production or seed output. In arid environments, crop varieties with early seedling vigor and good stand establishment tend to maximize use of available soil water, resulting in increased dry matter accumulation and improved grain yield. In temperate climates where lower soil temperature and higher moisture conditions often prevail at the time of planting, early sowing and use of minimum tillage exacerbate germination and seedling growth problems (Keim & Gardner, 1984). Seedling tolerance to low soil temperature is enhanced by vigorous seedling growth (Keim & Gardner, 1984).

Seedling vigor is a major breeding target in barley and other crops (Grando & Ceccarelli, 1995; Karrel *et al.*, 1993; Redoña & Mackill 1996a; Trachsel *et al*., 2010) because it is closely associated with crop growth and yield (Ellis, 1992). Simple traits such as seedling or plant height, seedling dry weight and kernel weight (Acevedo *et al.*, 1991; Regan *et al.*, 1992; Trachsel *et al*., 2010), rapid shoot growth, shoot dry weight and shoot length

(Williams & Peterson 1973; Sasahara *et al*., 1986; Grando & Ceccarelli 1995) have been identified as good indicators of a good seedling and early vigor in barley.

The coleoptile or shoot length plays an important role in stand establishment, particularly in rain-fed Mediterranean environments where cereals are often sown when the soil profile is dry. Deep sowing can minimize the risk of germination and subsequent death of the seedlings if drought immediately follows rainfall (Acevedo & Naji, 1987). However, deep sowing may have a negative effect on crop establishment if the coleoptile is not long enough to ensure the emergence of the first leaf.

Seed mass also can cause differences in biomass. Seed mass is more important than the relative growth rate (RGR) in determining early plant biomass in wild barley (Van Rijn *et al.*, 2000). In a study of the major factors responsible for variation in early vigor in barley, wheat, and oat, embryo size was found to be most important (López-Castaneda *et al*., 1996). Jurado and Westoby (1992) concluded that, among 28 native species from central Australia, seed size is more important than RGR or germination rate in determining seedling size 10 d after imbibition. Cisse & Ejeta (2003) reported that visual seedling scoring is a reliable method for estimating seedling vigor in sorghum. This trait also is important in other crops like maize (Revilla *et al.*, 1999) and rice (Sthapit & Witcombe, 1998).

For genetic improvement of early seedling growth, information on genetic variation in traits related to early seedling vigor and also knowledge concerning the relationships among various seedling vigor traits are necessary. Therefore, the objectives of this study were to (1) quantify the effect of seed weight on early seedling vigor, (2) assess the relationship among the traits, and (3) assess the extent and structure of genetic diversity for these traits in an ecogeographically diverse collection of wild barley.

Materials and methods

Plant materials: Three hundred and fifteen 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 polyhouse at the experimental farm at Chonbuk National University in Jeonju, Korea in 2007-2008. Seeds were harvested and stored at 4°C before analysis. The grains of all 315 accessions were stored at 40°C for one month before sowing and at the time of sowing at 4°C for 72 h to break possible dormancy. Grains of uniform and average size were selected for each accession per replication, and ten grains were used for seedling vigor assessments in the laboratory experiments.

Polyhouse experiment: An experiment employing a randomized complete block design with three replications was conducted in 2009-2010 in the polyhouse at Chonbuk National University to evaluate seedling vigor among the 315 accessions. Fertilization and other standard cultural practices recommended for barley cultivation at this location were used. Single row plots, each 1 m long and with 50 cm between rows, were used. Each plot was drill-seeded in the soil. Seeds were planted on 30 October in 2009 within the range of planting dates considered optimal for barley in South Korea. The average minimum and maximum soil temperatures at the 5-cm depth for the growing period were 4.3 and 13.5°C, respectively. The accessions were visually scored for seedling vigor on a scale of 1 (most vigorous) to 9 (least vigorous). These assessments were made at the 3- to 4-leaf stage, when differences in seedling vigor among accessions were the greatest. The visual scoring system is a relative evaluation based on the range of variation observed for seedling size in the collection and attempts to integrate seedling height, length and width of individual leaves. The observation on plant height in cm was taken on five arbitrarily selected plants at the same time.

Laboratory experiments: The hydroponic method of Myhill & Konzak (1967) was employed for seedling cultivation. Seeds were sown with the embryo side down between two sheets of wet thick filter paper (thickness 0.75 mm, weight 400 g/m^2, Schleicher and Schuell, Dasel, Germany) 6 cm high and 8 cm wide. After rolling up the sheets, the two distal edges were tied up with rubber bands to prevent the seeds from falling out. The resultant seed germination “sandwiches” were held up vertically in a plastic rack placed inside of a plastic box. Thus, ten seeds were located at the top of each filter paper sandwich, with the bottom half of the sandwich immersed in water. The plastic boxes were placed in a growth chamber in darkness at a temperature of 4°C for 72 h and then subjected to a photoperiod of 14 h at 20±2°C. The intensity of lighting was 350 µmol PAR $m^{-2}s^{-1}$. On the 8^{th} day after sowing, five uniform and representative seedlings were selected and measured for seedling length (mm); seedling fresh and dry weight (without seed) (mg); shoot length (mm); and shoot fresh and dry weight (mg). The seedling (without grain) and shoot were placed in individual coin envelopes and dried in an oven at 70°C until a constant weight was achieved. One hundred arbitrarily selected grains per accession were weighed to obtain the individual grains weight.

Data analysis: Principal Components Analysis (PCA) was used to reduce the dimensionality, and extract the maximum variance for all the traits. The scores of derived variables calculated for all the accessions were used to visualize the accession seedling vigor in 2- and 3-D PCA scatter plots. Relationships between pairs of measured traits were analyzed by the Pearson product-moment correlation. The PCA and Pearson correlation analyses were performed with SPSS (SPSS Inc., Chicago, Illinois, USA).

Results

The range, mean, standard error (SE) and coefficient of variation (CV) for all traits are given in Table 1 and show high among-accession variation for visual seedling vigor score and the other traits studied. The traits exhibiting the greatest variation were visual score (CV=33.0), plant height (CV=32.9), shoot fresh weight (CV=32.2), shoot dry weight (CV=30.7) and shoot length (CV=29.9). Seed weight exhibited the least variation (CV=16.0). The other traits showed intermediate levels of variation with CVs ranging from 23.4 to 26.8.

Relationship among seedling vigor traits: Highly significant correlations were detected among all the seedling traits (Table 2). However, seed weight showed only weak or no correlation with seedling traits (Table 2). The highest correlation coefficients (r=0.76-0.94) were observed in pairwise comparisons with seedling fresh weight, seedling dry weight, shoot fresh weight, shoot dry weight, and shoot length. Visual seedling score was significantly correlated with all the traits (albeit with relatively low r values of 0.10-0.53), except seedling length (Table 2).

Principal component analysis: The first three principal components explained 82.3% of the observed variation. PC1 accounted for 54.0% of variation and showed the largest loading values for shoot fresh weight, shoot dry weight, seedling dry weight, seedling fresh weight, shoot length and seedling length. PC2 and PC3 accounted for 17.1% and 11.1% of the observed variation, respectively. Plant height and visual seedling score contributed the most to PC2 and seed weight to PC3 (Table 3). Accessions WBDC020 (Turkey), WBDC238 (Jordan) and WBDC244 (Jordan) showed the highest seedling vigor among accessions on the basis of all traits combined (Fig. 1). Accessions with the highest positive values for most traits originated from the southwest portion of the Fertile Crescent, primarily in the countries of Jordan, Turkey, Israel, and Syria (Fig. 2). The PCA revealed a noticeable trend, viz. a overlap (despite a certain degree of separation) of accessions from the northern and southern part of the Fertile Crescent (Fig. 3). The accessions from Israel and Jordan were quite well separated from Turkey, Syria, Iran and Iraq on PC2. Among the Fertile Crescent countries, accessions from Lebanon showed the highest overlap between the two sub-regions (Fig. 3).

Table 1. Range of variation, mean, SE and CV for seedling vigor traits of 315 accessions from the Wild Barley Diversity Collection.

Traits	Min.	Max.	Mean	SE	CV
Seedling length (mm)	42.00	290.00	157.00	0.534	23.40
Seedling fresh weight (mg)	3.30	23.10	11.18	0.043	26.81
Seedling dry weight (mg)	0.2800	1.4400	0.8176	0.002	24.19
Shoot length (mm)	20.00	111.00	57.84	0.251	29.91
Shoot fresh weight (mg)	1.10	14.10	5.67	0.026	32.19
Shoot dry weight (mg)	0.1400	0.9400	0.4296	0.001	30.67
Visual seedling score	1	9	4.76	0.022	33.00
Plant height (cm)	6.00	43.00	23.27	1.112	32.86
Seed weight (g)	2.40	7.40	4.90	0.011	16.07

Table 2. Correlation among seedling vigor traits for 315 accessions from the Wild Barley Diversity Collection.

Traits	Plant height	Visual seedling score	Shoot dry weight	Shoot fresh weight	Shoot length	Seed weight	Seedling dry weight	Seedlings fresh weight
Visual seedling score	0.53***							
Shoot dry weight	0.24**	0.21**						
Shoot fresh weight	0.23**	0.22**	0.94***					
Shoot length	0.23**	0.10*	0.82***	0.84***				
Seed weight	0.09	0.28**	0.14*	0.15*	-0.04			
Seedling dry weight	0.17**	0.23**	0.84***	0.83***	0.65***	0.22**		
Seedling fresh weight	0.15*	0.23**	0.76***	0.81***	0.62***	0.23**	0.93***	
Seedling length	0.04	0.06	0.51***	0.55***	0.63***	-0.00	0.61***	0.68***

* p< 05; ** p < .01; *** p < .001

Table 3. Principal component analysis of seedling vigor traits in the Wild Barley Diversity Collection.

Component contribution variable	1st	2nd	3rd
Seedling length	0.76	-0.08	-0.07
Seedling fresh weight	0.89	0.06	0.26
Seedling dry weight	0.90	0.10	0.23
Shoot length	0.86	0.14	-0.21
Shoot fresh weight	0.92	0.17	0.06
Shoot dry weight	0.91	0.18	0.05
Visual seedling score	0.08	0.80	0.30
Plant height	0.11	0.90	-0.09
Seed weight	0.06	0.11	0.93
Total variance explained (%)	54.07	17.11	11.18
Accumulated variance (%)	54.07	71.18	82.37

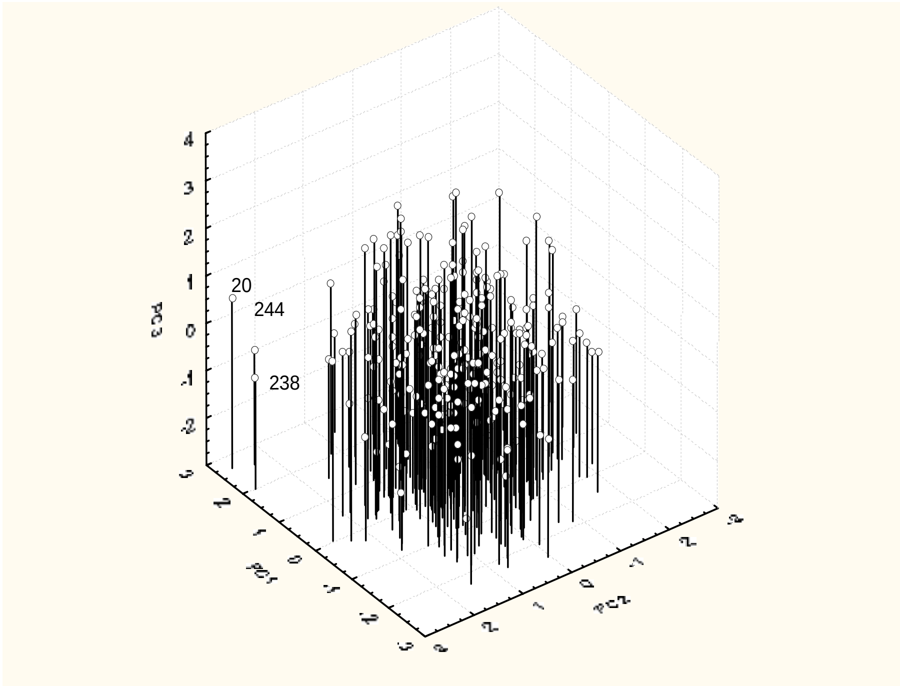

Fig. 1. Principal component analysis of seedling vigor traits in the Wild Barley Diversity Collection. Axes are the three principle components, PC1, PC2 and PC3. Key to outlying accessions 20=WBDC020; 238=WBDC238 and 244= WBDC244.

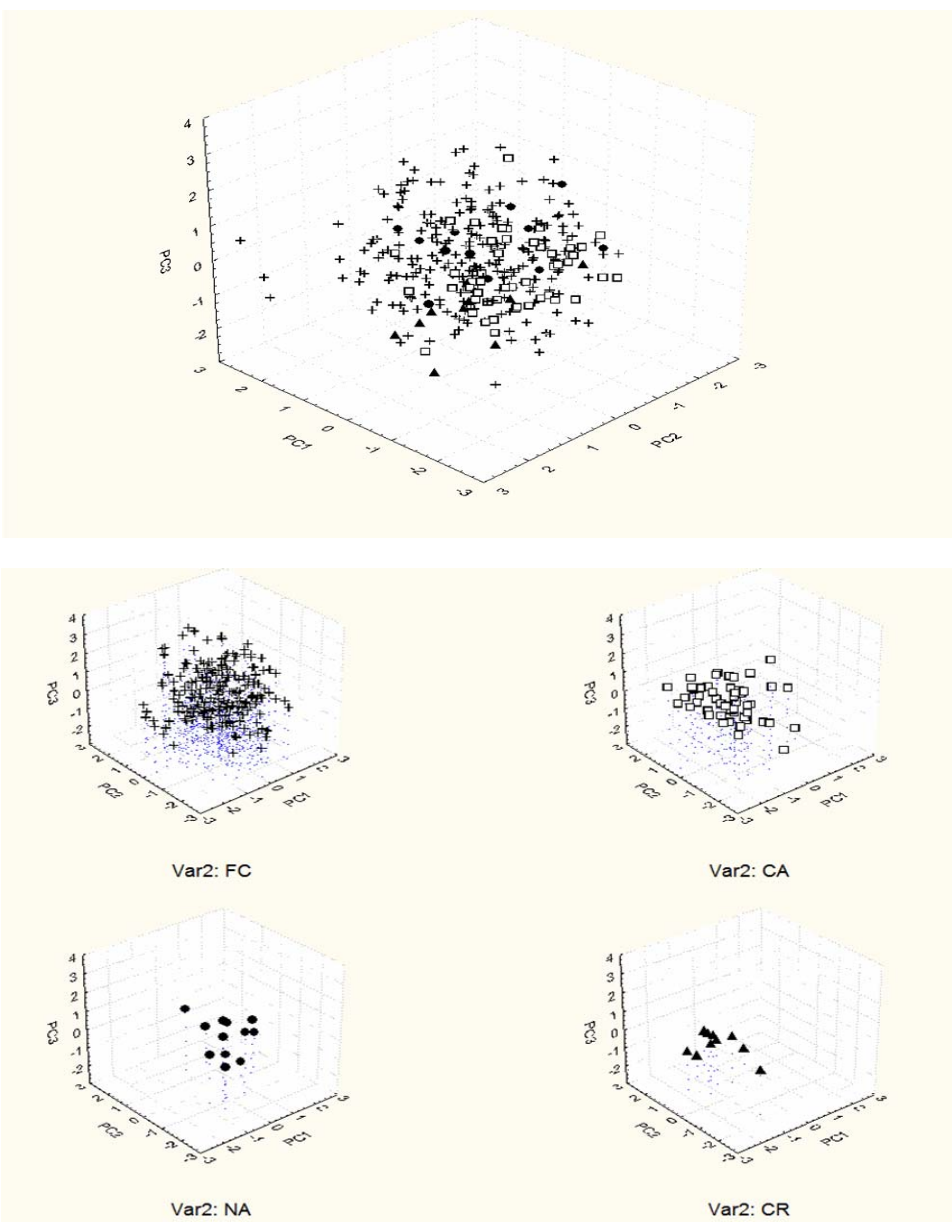

Fig. 2**.** Principal component analysis of seedling vigor traits in geographical origins (Fertile Crescent, FC; Central Asia, CA; North Africa, NA; and Caucasus region, CR). Axes are the three principle components, PC1, PC2 and PC3.

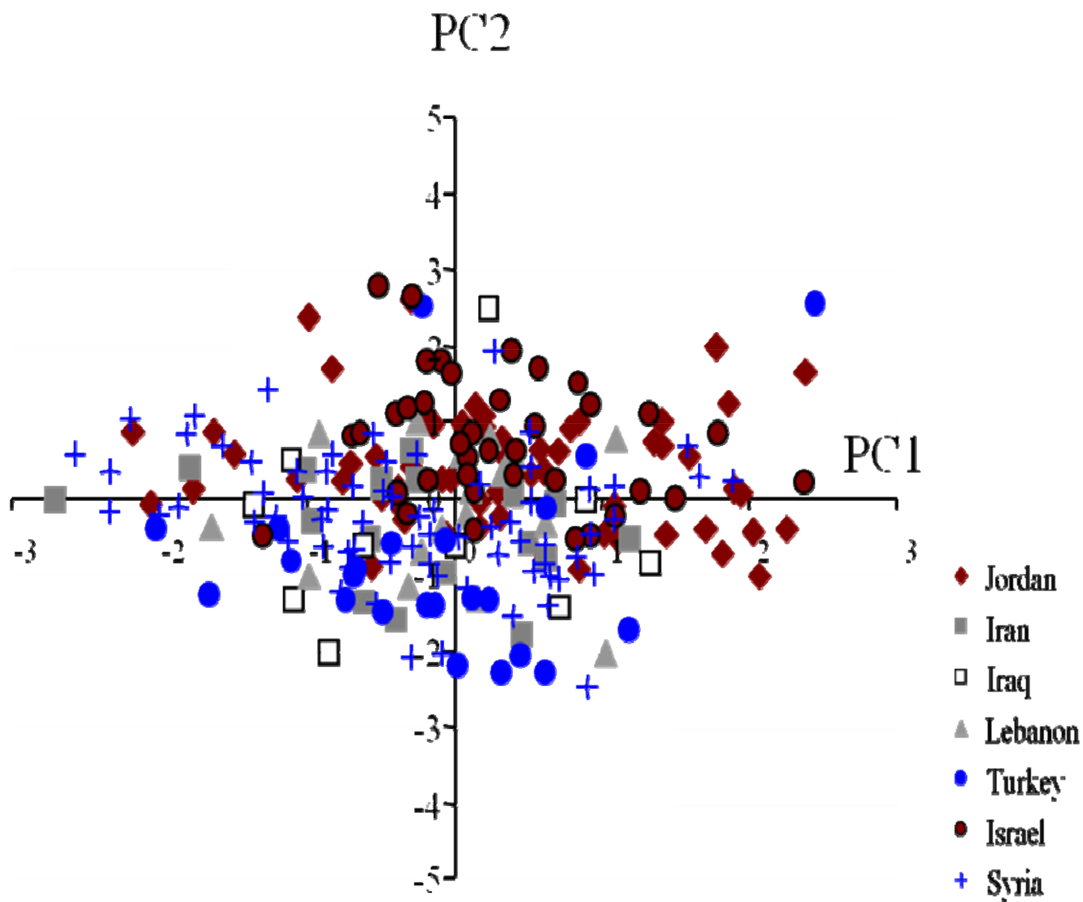

Fig. 3. Principal component analysis of seedling vigor traits of accessions from the Fertile Crescent. Axes are the two principle components, PC1and PC2.

Discussion

In this investigation, we observed a wide range of variation among the WBDC accessions for all seedling vigor traits examined. The level of variation observed was considerably higher than previously reported in wild barley. Grando and Ceccarelli (1995) observed low variation for mean seed weight (2.8 g with range of 1.9-3.6 g), while we found a higher mean (4.9 g) and wider range (range 2.4 g – 7.4 g). Similar results also were found for shoot dry weight. The low variation found by the previous investigators may have been due to limited number of accessions used (19) compared to the current study where 315 accessions from 19 different countries were utilized. High variations were also found for seedling vigor traits in sorghum (Cisse & Ejeta, 2003), rice (Cui *et al.*, 2002) and maize (Trachsel *et al.*, 2010).

The visual seedling score was significantly correlated with plant height, seed weight, shoot length and seedling and shoot fresh and dry weight. Significant correlation between seedling vigor scores and plant height as well as kernel weight were reported in corn (Revilla *et al.*, 1999), while vigor scores in rice were significantly correlated with percentage germination, plumule vigor, and greening (Sthapit & Witcombe, 1998) and with seedling height and weight in sorghum (Cisse & Ejeta, 2003). Therefore, the visual seedling score can be a method for estimating seedling vigor in wild barley.

In this study, we found a positive correlation between seed weight and seedling dry weight. Seedling dry weight is known to correlate positively with seed weight (Van Andel & Biere, 1990; Van Rijn *et al.*, 2000; Cui *et al.*, 2002) because at the initial stage of seedling growth, growth is largely dependent on the seed reserve (Yoshida, 1981). Positive correlation between seed and seedling weight was observed in rice (Cui *et al.*, 2002; Lu *et al.*, 2007), but not in sorghum and wheat (Radford & Henzell, 1990; Mian & Nafziger, 1992). Revilla *et al.*, (1999) found maternal effects for kernel weight on early field vigor and plant weight in maize, and recommended that accessions with larger kernel weight be used as the seed parent in breeding to improve early vigor. In maize, kernel weight was moderately correlated with leaf dry weight and shoot dry weigh (Trachsel *et al.,* 2010). Therefore, at least in some crops, seed weight can be used as a selection criterion for rapid seedling establishment.

The accessions from the Fertile Crescent (especially from Jordan, Israel, Turkey and Syria) showed good seedling vigor (Fig. 2). Jana and Pietrzak (1988) suggested that genetic resources of wild barley in the Fertile Crescent can be exploited for improvement of cultivated barley. Similarly, Feuillet *et al.*, (2007) suggested the importance of regional landraces, local cultivars and related species as having a beneficial role for crop improvement. Many major genes have been transferred from wild relatives into the many cultivated crops as concrete examples of exploiting biodiversity (Hajjar & Hodgkin, 2007). 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).

Accessions WBDC020 from Turkey and WBDC238 and WBDC244 from Jordan exhibited the highest positive values among the wild barley accessions for most of the seedling vigor traits. These accessions may be useful as parents in breeding programs for seedling vigor in both arid environments and temperate regions. Ludlow & Muchow (1990) suggested that early vigor should be considered an essential component of crop plant development under most environmental conditions. The early growth of seedlings is crucial for their establishment and biomass production. In arid environments, crop varieties with early seedling vigor and good stand establishment tend to maximize use of available soil water, resulting in increased dry matter accumulation and improved grain yield. Keim & Gardner (1984) reported that seedling tolerance to low temperature is enhanced by vigorous seedling growth.

Conclusions

Early seedling vigor is an important complex trait in barley and other field crops. This is the first study of early seedling vigor traits in a large and ecogeographically diverse collection of wild barley germplasm. Results show a wide variation for all the seedling vigor traits among the accessions. We found that a visual seedling score was a reliable method for estimating seedling vigor in wild barley. Accessions from the Fertile Crescent (especially from Jordan, Israel, Turkey and Syria) possessing good early seedling vigor traits may be useful as valuable genetic resources for the improvement of seedling vigor traits in cultivated barley. In particular, WBDC020 (Turkey), WBDC238 (Jordan) and WBDC244 (Jordan) had among the highest positive values for the most traits and may be useful as parents in transferring positive alleles for multiple seedling vigor traits.

Acknowledgements

This work was supported by a grant (Code #20070301034043) from BioGreen 21 Program, Rural Development Administration, Republic of Korea to KJ Lee, a grant from Regional Subgenebank Support Program of RDA, Republic of Korea to SJ Yun and the Lieberman-Okinow Endowment to BJ Steffenson at the University of Minnesota. We thank Dr. Joy K. Roy for helpful discussions and information regarding the wild barley collection.

References

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

Acevedo, E. and I. Naji. 1987. Variation in coleoptile length of barley, durum wheat and bread wheat genotypes. *In*: *Cereal Improvement Program*. Annual Report for 1986, ICARDA, Aleppo, Syria, pp. 153-156.

Acevedo, E., P.O. Crawfurd, R.B. Austin and P. Perez-Marco. 1991. Traits associated with high yield in barley in low-rainfall environments. *J. Agric. Sci.*, 116: 23-36.

Cui, K.H., S.B. Peng, Y.Z. Xing, S.B. Yu and C.G. Xu. 2002. Molecular dissection of relationship between seedling characteristics and seed size in rice. *Acta. Bot. Sin.*, 44: 702-707.

Cisse, N. and G. Ejeta. 2003. Genetic variation and relationship among seedling vigor traits in sorghum. *Crop Sci.*, 43: 824-828.

Van Rijn, C.P.E., I. Heersche, Y.E.M.V. Berkel, E. Nevo, H. Lambers and H. Poorter. 2000. Growth characteristics in *Hordeum spontaneum* populations from different habitats. *New Phytol.*, 146: 471-481.

Ellis, R.H. 1992. Seed and seedling vigor in relation to crop growth and yield. *Plant Growth Regul.*, 11: 249-255.

Ellis, R.P., B.P. Forster, D. Robinson, L. Handley, D.C. Gordon, J.R. Russell and W. Powell. 2000. Wild barley: a source of genes for crop improvement in from a wild rice relative, the 21st century? J. *Exp. Bot.*, 51: 9-17.

Feldman, M. and E.R. Sears. 1981. The wild gene resources of wheat. *Sci. Am.*, 244: 98-108.

Feuillet, C., P. Langridge and R. Waugh. 2007. Cereal breeding takes a walk on the wild side. *Trends Genet.*, 24: 24-32.

Grando, S. and S. Ceccarelli. 1995. Seminal root morphology and coleoptiles length in wild (*Hordeum vulgare* ssp. *sontaneum*) and cultivated (*Hordeum vulgare* ssp *vulgare*) barley. *Euphytica*, 86: 73-80.

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.

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.

Hund, A., Y. Fracheboud, A. Soldati, E. Frascaroli, S. Salvi and P. Stamp. 2004. QTL controlling root and shoot traits of maize seedlings under cold stress. *Theor. Appl. Genet*., 109: 618-629.

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.

Jurado, E. and M. Westoby. 1992. Seedling growth in relation to seed size among species of arid. *Australia J. Ecol.*, 80: 407-416.

Karrel. E.E., J.M. Chandler, M.R. Foolad and R.L. Rodrigue. 1993. Correlation between α-amylase gene expression and seedling vigor in rice. *Euphytica*, 66: 163-169.

Keim, K.R. and C.O. Gardner. 1984. Genetic variation for cold tolerance in selected and unselected maize populations. *Field Crops Res.*, 81: 43-151.

López-Castaneda, C., R.A. Richards, G.D. Farquhar and R.E. Williamson. 1996. Seed and seedling characteristics contributing to variation in early vigor among temperate cereals. *Crop Sci*., 36: 1257-1266.

Lu, X.L., A.L. Niu, H.Y. Cai, Y. Zhao, J.W. Liu, Y.G. Zhu and Z.H. Zhang. 2007. Genetic dissection of seedling and early vigor in a recombinant inbred line population of rice. *Plant Sci.*, 172: 212-220.

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

Mian, A.R. and E.D. Nafziger. 1992. Seed size effects on emergence, head number, and grain yield of winter wheat. *J. Prod. Agric.*, 5: 265-268.

Myhill, R.R. and C.E. Konzak. 1967. A new technique for culturing and measuring barley seedlings. *Crop Sci.*, 7: 275-276.

Petersen, L., H. Ostergard and H. Giese. 1994. Genetic diversity among wild and cultivated barley as revealed by RFLP. *Theor. Appl. Genet.*, 89: 676-681.

Radford, B.J. and R.G. Henzell. 1990. Temperature affects the mesocotyl and coleoptile length of grain sorghum genotypes. *Aust. J. Agric. Res.*, 41: 79-87.

Redoña, E.D. and D.J. Mackill. 1996a. Genetic variation for seedling vigor traits in rice. *Crop Sci.*, 36: 285-290.

Regan, K.L., K.H.M. Siddique, N.C. Turner and B.R. Whan. 1992. Potential for increasing early vigor and total biomass in spring wheat. 2. Characteristics associated with early vigor. *Aust. J. Agric. Res.*, 43: 541-553.

Revilla, P., A. Butro´n, R.A. Malvar and A. Orda´s. 1999. Relationships, among kernel weight, early vigor, and growth in maize. *Crop Sci.*, 39: 654-658.

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.

Sasahara, T., H. Ikarashi and M. Kambayashi. 1986. Genetic variations in embryo and endosperm weights, seedling growth parameters and α-amylase activity of the germinated grains in rice (*Oryza sativa* L.). *Jpn. J. Breed.*, 36: 248-261.

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. Agri. Res.*, 58: 532-544.

Sthapit, B.R. and J.R. Witcombe. 1998. Inheritance of tolerance to chilling stress in rice during germination and plumule greening. *Crop Sci.*, 38: 660-665.

Trachsel, S., R, Messmer, P. Stamp, N. Ruta and A. Hund. 2010. QTLs for early vigor of tropical maize. *Mol. Breed.*, 25: 91-103.

Van Andel, J. and A. Biere. 1990. Ecological significance of variability in growth rate and plant productivity. In: *Causes and consequences of variation in growth rate and productivity in plants*. (Eds.): H. Lambers, M.L. Cambridge, H. Konings, T.L. Pons. SPB Academic Publishing, The Hague, The Netherlands, pp. 257-268.

Volis, S., S. Mendlinger, Y. Turuspekov, U. Esnazarov, S. Abugalieva and N. Orlovsky. 2001. Allozme variation in Turkmenian populations of wild barley, *Hordeum spontaneum* Koch. *Annals of Bot.*, 87:435-446.

Volis, S., S. Mendlinger, Y. Turuspekov and U. Esnazarov. 2002. Phenotypic and allozyme variation in Mediterranean and desert populations of wild barley, *Hordeum spontaneum*. *Evolution*, 56: 1403-1415.

Volis, S., B. Yakubov, I. Shulgina, D. Ward and S. Mendlinger. 2005. Distinguishing adaptive from non-adaptive genetic differentiation: comparison of Q_{ST} and F_{ST} at two spatial scales. *Heredity*, 95: 466-475.

Volis, S., I. Shulgina, M. Zaretsky and O. Koren. 2010. Epistasis in a predominantly selfing plant. Heredity (advance online publication 16 June 2010; doi: 10.1038/hdy.2010.79)

Whabi, A. and P.J. Gregory. 1989. Genotypic differences in root and shoot growth of barley (*Hordeum vulgare*) I. Glass house studies of young plants and effects of rooting medium. *Expt. Agriculture*, 25: 375-387.

Williams, J.F. and M.L. Peterson. 1973. Relation between alpha-amylase activity and growth of rice seedlings. *Crop Sci.*, 13: 612-614.

Yoshida, S. 1981. *Fundamentals of rice crop science*. IRRI, Los Banos, The Philippines.

Zohary, D. 1969. The progenitors of wheat and barley in relation to domestication and agricultural dispersal in the old world. *In*: Ucko, P.J. and G.W. Dimbleby (Ed.), *The domestication and exploitation of plants and animals*. Gerald Duckworth and Co. Ltd., London, pp. 47-66.

(Received for publication 20 December 2010)