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Genetic variation for agronomic characters and drought tolerance among the recombinant inbred lines of wheat from the Norstar × Zagross cross

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Abstract

Interest in developing drought tolerant varieties is growing due to global warming. Identification of genetic variability for drought tolerance is a prerequisite to achieve this objective. In this study a sample of 28 recombinant inbred lines (RILs) of wheat developed from the cross of Norstar and Zagross varieties, together with their parents, were evaluated for two years (2010-2012) under normal and water stress conditions using split plot design with three replications. Main plots included two irrigation treatments of 70 and 140 mm evaporation from Class A pan and sub-plots consisted of 30 genotypes. The effect of genotypes and interaction of genotypes with years and water regimes were significant for all characters. Significant genotypic effect implies the existence of genetic variation among the lines under study. Heritability estimates were high for 1000 grain weight (0.87), flag leaf area (0.84), and days to heading (0.82). Biomass, grain yield, and straw yield showed the lowest heritability values (0.42, 0.50, and 0.51, respectively). Moderate genetic advance for most of the traits suggested the feasibility of selection among the RILs under investigation. Some RILs were higher yielding than either parent at both environments. Transgressive segregation was also observed for geometric mean productivity (GMP) and stress tolerance index (STI), indicating the possibility of selecting lines that are more drought tolerant than Norstar and Zagross varieties. Cluster analysis based on yield in the normal and water stress conditions, STI, and GMP identified six promising lines that can be evaluated further for drought tolerance in more environments.

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Introduction

Environmental stresses are either biotic or abiotic. Plants in the field are exposed to different abiotic stresses such as water deficit, cold, heat, and salinity. It is estimated that theses stresses could reduce the crop yield by more than 50% (Vij and Tyagi, 2007). Water stress is the major limiting factor in crop production worldwide. Wheat is a relatively sensitive crop to water stress and available soil water. Drought stress may occur throughout the growing season, early or late, but its effect on yield reduction is highest when it occurs after anthesis (Blum, 2005). Water deficit reduces yield (Benmousa and Achouch, 2005; Hamam, 2008; Sanjari Pireivatlou and Yazdansepas, 2008) by affecting its components. It has been reported that water deficit has adverse effect on number of kernels per spike (Beltrano *et al.*, 2006; Akram, 2011), 1000 kernel weight (Beltrano *et al.*, 2006; Hamam, 2008; Mastrangelo *et al.*, 2008), and number of spikes per meter area (McDonald *et al.*, 1984; Moayedi *et al.*, 2010).

Risk management is crucial in the investment and financing decisions for farmers in developing countries and in transition economies. Basic risk management in agriculture includes choosing plant varieties against adverse weather events (Roberts, 2005). The optimum variety should have superiority in environments with different stress intensities. Some genotypes are only favorable in a specific environment, like landraces which have been adapted for sever local stresses or inbred cultivars which have been genetically modified for high yield in full irrigation conditions. The plant performance in diverse environments depends on efficiency of developed varieties which should be matched to the production area. Multi-environment testing is the main tool for understanding varietal responses to the environments, although the process is time-consuming and expensive.

Development of stress tolerant varieties is always a major objective of many breeding programs but success has been limited by the low heritability of grain yield, existence of genotype by environment interaction, and lack of adequate screening techniques. Therefore, wheat breeders are always looking for means and sources of genetic improvement for grain yield and other agronomic traits. Understanding the plant response in dry environments has great importance and is a fundamental part of producing stress tolerant crops (Reddy *et al.*, 2004; Zhao *et al.*, 2008).

Drought tolerance was defined by Hall (1993) as the relative yield of a genotype compared to other genotypes, subjected to the same drought stress condition. In this regard several indices have been utilized to evaluate genotypes for drought tolerance based on grain yield in different environments. Some of them are as follow. Rosielle and Hamblin (1981) defined stress tolerance (TOL) index as the differences in yield between the stress (Ys) and non-stress (Yp) environments and mean productivity (MP) as the average yield of Ys and Yp. Fischer and Maurer (1978) proposed a stress susceptibility index (SSI) for cultivars. Fernandez (1992) defined a stress tolerance index (STI), which can be used to identify genotypes that produce high yield under both stress and non-stress conditions. The other yield based index for drought resistance is geometric mean productivity (GMP). The geometric mean is often used by breeders interested in relative performance, since drought stress can vary in severity in field environments over years (Ramirez Vallejo and Kelly, 1998).

The lines under investigation were a part of a larger set of recombinant inbred lines developed from the cross of Norstar and Zagross varieties for the purpose of genetic studies and possible development of new varieties. Due to global warming, drought tolerance is being regarded as one of the important characters in many breeding programs. So far, the studied lines have not been evaluated for response to water stress. Therefore, the objectives of this work were to identify the high yielding and drought tolerant winter genotypes and also determine genotype by environment interaction, estimate heritability, and predict genetic advance among these recombinant inbred lines.

Materials and methods

Plant materials and experimental design

The field experiments were conducted at Agricultural Research Station of Islamic Azad University of Tabriz, located in the northwest of Iran (38° 5´ N and 46° 27´ E, 1360 m altitude) during two cropping seasons (2010-2011 and 2011-2012). Some climatic parameters during the experiment are given in Table 1. The soil texture was clay-loam with less than 1% of organic matters.

In each year, 28 recombinant inbred lines of wheat randomly sampled from a larger population, together with their parental varieties, Norstar (a winter type variety developed in Canada) and Zagross (a spring type and relatively drought tolerant variety developed in Iran), were evaluated under two irrigation conditions, using a split plot design based on randomized complete blocks with three replications. Main plots included irrigation treatments at two levels: 70 and 140 mm evaporation from Class A pan for normal and drought stress conditions, respectively. Plots were arranged in three rows of two- meters long and 15 cm apart. Cultural practices were carried out according to the existing standards. During the growing season, days to heading, plant height, spike length, biomass, flag leaf area, kernel number per spike, 1000-grain weight, straw yield, harvest index, and grain yield were recorded in each experiment.

Analysis of variance was carried out by combining the data from two years of experimentation. Normality of experimental errors was checked by the Shapiro-Wilk's normality test. Where the normality assumption was not fulfilled, a log transformation was performed. However, for the leaf area and plant height none of the data transformation methods were useful and thus we used bootstrapping for the data analysis. Furthermore, based on residual plots, weighted least squares method was carried out for the analysis of 1000-grain weight, days to heading, and kernel number per spike due to heteroscedasticity.

Statistical analyses

Heritability estimates were obtained using variance components as below:

$$h^2 = \frac{\sigma_g^2}{\left(\sigma_g^2 + \frac{\sigma_e^2}{ry}\right)}$$

where, σ^2_g= genetic variance; σ^2_e = environmental variance; r = number of replications; y = number of environments

Genetic advances for the characters under study were calculated following as below (Allard, 1960):

GA = $\sigma_p \times h^2 \times k$

where, σ_p = standard deviation of the phenotypic variance; h^2 = narrow sense heritability;

k = standardized selection intensity (regarding 10% selection intensity k = 1.755).

Genotypic coefficient of variation (CV_g) and phenotypic coefficient of variation (CV_p) were calculated by the following formula:

$$CV_g = \frac{\sqrt{\sigma_g^2}}{\overline{X}_{oo}} \times 100$$

$$CV_p = \frac{\sqrt{\sigma_p^2}}{\overline{X}_{oo}} \times 100$$

where, X_{oo} is the grand mean for each character.

In order to determine the tolerance of recombinant inbred lines under study we used Geometric Mean Productivity (GMP) (Rosielle and Hamblin, 1981) and Stress Tolerance Index (STI)(Fernandez, 1992) indices as follows:

$$GMP = \sqrt{Y_P \times Y_S}$$

STI= $(Y_p \times Y_s)/(\overline{Y}_P)^2$

where, Y_P is the mean grain yield of the genotype under non-stress condition, Y_S is the mean grain yield under water stress condition and $\overline{Y}_P$ is the mean grain yield of all genotypes under non-stress condition. GMP and STI have been shown mostly to be suitable indices for selecting drought tolerant genotypes (Fernandez, 1992; Mohammadi *et al.*, 2011a).

Furthermore, cluster analysis of the genotypes based on yield in the normal and water stress conditions, STI, and GMP was carried out using the average linkage algorithm and Euclidean distance measure for the purpose of defining higher yielding groups of recombinant inbred lines with more drought tolerance. Number of clusters was pre-determined as 4 by $(n/2)^{1/2}$, where n is the number of genotypes under study (Romesburg, 2004).

Data were analyzed by MSTAT-C and SPSS computer packages.

Results and discussion

Analysis of variance for agronomic characters

Combined analysis of variance showed the significant effects of year, genotype, year × water regime, genotype × year, genotype × water regime and genotype × water regime × year for all of the characters under study (Table 2). The results indicate considerable genetic variability among the recombinant inbred lines of wheat under study for all of the characters including grain yield, suggesting that the parents used in the cross were genetically different. Environmental conditions were not also similar in two years, specially, in terms of rainfall distribution and temperature. Significant interaction of genotypes with water regimes and years suggest that the differences among genotypes were not stable across water regimes and years. Genotype by environment interaction (GEI) has been observed in many studies. GEI is important in crop breeding and production (Kang and Gauch, 1996). GEI confounds with the genotypic effects if the experiment is carried out in only one environment. GEI has a negative impact on heritability. The lower the heritability of a trait, the greater the difficulty in improving that trait via selection (Yan and Kang, 2003). Knowledge about GEI is important because a significant GEI can seriously impair selecting superior genotypes in plant breeding programs (Shafii and Price, 1998). Information about GEI is useful to plant breeders in deciding whether to develop a cultivar for all environments or to develop specific genotypes for specific environments (Bridges, 1989).

Table 1. Rainfall and mean temperature during 2010-2012 growth seasons at Tabriz Agricultural Research Station of Islamic Azad University.

Climatic parameters	Year	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	Total
Rainfall	2010-11	7.0	0.0	1.1	7.8	18.3	42.4	85.7	35.0	0.7	198
	2011-12	13.7	26.7	7.9	25.2	42.1	20.0	26.7	27.5	15.8	205.6
Mean temp. (°C)	2010-11	17.1	8.8	4.4	-0.7	1.7	6.5	12.8	17.9	24.9	
	2011-12	13.7	2.9	-0.8	0.0	2.5	3.2	14.8	19.8	25	

Estimates of genetic parameters

Estimates of genotypic and phenotypic variances, genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV), narrow sense heritability among lines, and genetic advance per se and expressed as percentage of the mean for the studied attributes are presented in Table 3. In all characters, the PCV was larger than GCV, however, in some cases the differences were negligible. Highest genotypic and phenotypic coefficients of variation belonged to flag leaf area and straw yield. Although significant differences were observed among the recombinant inbred lines for days to heading and spike length, the values for PCV, GCV, and also genetic advance were low, indicating that improvement for these characters may not be effective in this population. Similar results for days to heading were observed by Ehdaie and Waines (1989), Belay *et al.* (1993), and Moghaddam *et al.* (1998). High heritability estimates were obtained for 1000 grain weight (0.87), flag leaf area (0.84), and days to heading (0.82). The estimate was relatively high for the number of kernels per spike (0.71). High heritability estimates in wheat have been reported in most studies for 1000 grain weight (Ehdaie and Waines, 1989; Moghaddam *et al*., 1997; Moghaddam *et al.,* 1998; Ali and Shakor, 2012; Koumber and El-Gammaal, 2012), flag leaf area (Khan and Naqvi, 2011), days to heading (Ehdaie and Waines, 1989; Moghaddam *et al*., 1997; Moghaddam *et al*., 1998; Khan and Naqvi, 2011), and kernels per spike (Ehdaie and Waines, 1989; Moghaddam *et al.,* 1997; Moghaddam *et al*., 1998; Mohammadi *et al*., 2011b). Days to heading and 1000 grain weight are less sensitive to environmental effects and therefore showed high heritability in most studies. Biomass, grain yield, and straw yield had the lowest heritability values (0.42, 0.50, and 0.51, respectively) among the traits studied. Moderate to low heritability estimates for grain yield were also reported by others (Gandhi *et al*., 1964; Ehdaie and Waines, 1989). Lower heritability values for grain yield as compared with the estimates for the yield components in our study and other researches (Ehdaie and Waines, 1989; Belay *et al*., 1993; Moghaddam *et al*., 1997; Moghaddam *et al*., 1998) indicate the important contribution of environmental effects to the phenotypic variance of this trait. Therefore, selection for grain yield per se in the segregating generations would not be fruitful and emphasis must be put on the components such as 1000 grain weight and number of kernels per spike. Moderate genetic gain for most of the characters suggests that selection for superior genotypes would be effective among the recombinant inbred lines obtained from the cross of Norstar and Zagross varieties.

Table 2. Analysis of variance of different agronomic characters for 28 recombinant inbred lines of wheat and two parental varieties under two water regimes during 2010-11 and 2011-12 growing seasons.

		Mean squares (based on log transformation)				
SOV	df	Spike length	Biomass	Grain yield	Straw yield	Harvest index
Year (Y)	1	0.054**	2.796**	4.122**	2.100**	0.115*
Replication/Y	4	0.005**	0.062**	0.120**	0.064**	0.035**
Water regime (W)	1	0.175 ns	1.567**	0.015 ns	1.345ns	0.017 ns
W × Y	1	0.008**	0.010**	0.108**	0.105**	0.003**
Error A	4	0.003	0.014	0.007	0.022	0.005
Genotype (G)	29	0.003**	0.016**	0.019**	0.029**	0.016**
G × Y	29	0.003**	0.013**	0.014**	0.019**	0.008**
G × W	29	0.001**	0.010**	0.012**	0.017**	0.008**
G× W×Y	29	0.001**	0.009**	0.009**	0.016**	0.007**
Error B	232	0.001	0.007	0.006	0.011	0.004

ns, * and **: Non-significant and significant at 5% and 1% levels of probability, respectively

Table 2 continued

SOV	df	Mean squares				
		Based on bootstrapping		Based on weighted least squares		
		Plant height	Flag leaf area	Days to heading	Kernel number per spike	1000-grain weight
Year (Y)	1	58909.3**	18798.4**	29831.6**	761.4*	1610.0**
Replication/Y	4	207.1**	241.9**	230.2**	293.3**	34.4**
Water regime (W)	1	18762. 7 ns	59.3ns	48.4ns	5733.4ns	988. 9ns
W × Y	1	875.7**	136.8**	235.3**	223.3**	24.8**
Error A	4	136.2	4.9	135.8	93.2	71.3
Genotype (G)	29	273.6**	78.2**	782.8**	261.5**	330.8**
G × Y	29	72.7**	96.5**	302.6**	374.7**	93.7**
G × W	29	62.74**	13.47**	82.16**	127.29**	44.56**
G× W×Y	29	43.00**	9.63**	62.13**	224.52**	94.46**
Error B	232	58.00	6.98	30.85	38.40	19.67

ns, * and **: Non-significant and significant at 5% and 1% levels of probability, respectively.

Drought tolerance

Grain yield under normal (Yp) and water stress (Ys) conditions, geometric mean productivity (GMP), and stress tolerance index (STI) for 28 recombinant inbred lines of wheat and the two parental varieties based on the average of two growing seasons are presented in Table 4. Grain yield ranged from 349.95 (Norstar) to 508.16 (Line No. 95) grams per meter square in the normal environment and from 214.78 (Line No. 31) to 381.07 (Line No. 95) grams per meter square in the water stressed condition suggesting considerable variability among the recombinant inbred lines under both conditions. This indicates the possibility of selection for suitable genotypes in the normal and water stressed environments. Most of the recombinant inbred lines were higher yielding than either parent at both water regimes, implying the existence of transgressive segregation in the cross of Norstar and Zagross varieties. Transgressive segregation has been reported in many studies (Vega and Frey, 1980; Zwer and Qualset, 1991; Rieseberg and Ellstrand, 1993; Fabrizius *et al.,* 1998; Rieseberg *et al.*, 1999; Valeriu *et al.*, 2012; Yang *et al.*, 2012; Zhang, 2013). This phenomenon enables the breeders to select genotypes superior to the parental lines and develop new improved varieties. Rieseberg *et al.* (1999) surveyed 113 studies in plant species and showed that transgressive segregation is the rule rather than the exception. In addition they indicated that the frequency of transgressive segregation in inbred species was higher than outbred species because fixed differences required for transgressive segregation will build up more rapidly between selfing than outcrossing populations. Complementary gene action has been proposed as the primary cause of transgressive segregation (Vega and Frey, 1980; Li *et al.*, 1995; Bradshaw *et al.*, 1998; Rieseberg *et al.*, 1999). Transgression was also observed for GMP and STI. Most of the recombinant inbred lines were more drought tolerant than either parent on the average of two years, suggesting the possibility of selecting recombinant inbred lines that are more tolerant to water deficit than Norstar and Zagross varieties. Transgressive segregation for drought tolerance and related traits in wheat and other crops has been reported also by several investigators (Yue *et al.*, 2006; Khanna –Chopra *et al.*, 2012; Sabadin *et al.,* 2012). For example, Khanna –Chopra *et al.* (2012) evaluated 206 recombinant inbred lines of wheat, resulted from the cross of two cultivars WL711 and C306, under normal and water stress conditions by withholding irrigation in the latter environment from 2007 to 2010. They used drought susceptibility index (DSI) as the selection criterion for drought tolerance. DSI of yield and yield components showed considerable variation and transgressive segregation in the recombinant inbred line population. Based on DSI of yield and yield components of the medium to late flowering lines, eight recombinant inbred lines were identified for combining yield higher than C306 with yield stability. In our experiment Line 95 had the highest STI (1.06) and GMP (404.05) among the lines under study. As was indicated earlier, Line 95 showed highest grain yield at both normal and water stress environments. This line had the second highest 1000-grain weight (43.29 grams). Seven lines (No. 68, 46, 8, 93, 143, 183, 23) showed also higher GMP and STI than other lines. Their STI value ranged from 0.94 to 0.80 which were higher than Norstar (0.53) and Zagross (0.62). The superiority of lines 46, 8, 93, and 23 was mainly due to higher 1000- grain weight (43.49, 40.61, 43.25, and 43.01 grams, respectively) as compared to the grand mean of the genotypes (39.1 grams). On the other hand, higher kernel number per spike contributed to the higher grain yield of lines 143 and 183 (35.36 and 36.27) relative to grand mean (33.88). It seems that different yield components contribute to the grain yield superiority of different genotypes.

Cluster analysis

Cluster analysis of the recombinant inbred lines based on yield in the normal and water stress conditions, STI, and GMP (Figure 1), located Line No. 95 in a separate cluster. Of the seven lines mentioned above, lines 68, 46, 8, 93, and 143 were grouped together in another cluster with the average STI and GMP of 0.88 and 400.43, respectively. These promising genotypes should be further investigated for drought tolerance under different environmental conditions. Wheat breeders have made significant improvements in adaptation of wheat to stress-prone environments (Trethowan *et al.*, 2002; Lantican *et al.*, 2003). This success has largely been achieved through field-based empirical selection for stress tolerance.

Table 3. Genetic variance (σ^2_g), phenotypic variance (σ^2_p), genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV), narrow sense heritability among lines (h^2), and expected genetic advance (GA) for the traits under study for 28 recombinant inbred lines of wheat and two parental varieties evaluated at two water regimes and two years.

Trait	σ^2_g	σ^2_p	GCV%	PCV%	h^2	GA	GA (% of the mean)
Days to heading	6.52	7.93	1.13	1.24	0.82	4.10	1.79
Plant height	17.97	27.64	5.35	6.63	0.65	5.98	7.54
Flag leaf area	5.93	7.10	11.06	12.11	0.84	3.93	17.84
Spike length	0.08	0.13	3.22	4.28	0.57	0.36	4.23
Kernel number per spike	3.62	5.10	5.62	6.87	0.71	2.81	8.29
1000-grain weight	8.19	9.39	7.32	7.84	0.87	4.66	11.92
Grain yield	699.71	1397.39	6.91	9.76	0.50	32.71	8.54
Biomass	3912.81	9362.64	5.87	9.08	0.42	71.12	6.66
Straw yield	3860.42	7671.02	9.09	12.81	0.51	78.17	11.43
Harvest index (%)	6.93	12.35	7.32	9.78	0.56	3.44	9.57

Table 4. Grain yield under normal (Yp) and water stress (Ys) conditions, geometric mean productivity (GMP), and stress tolerance index (STI) for 28 recombinant inbred lines of wheat and the two parental varieties based on the average of two growing seasons.

Line No.	Yp (g/m^2)	Ys (g/m^2)	GMP	STI
1	440.55	274.79	347.93	0.66
8	439.54	356.45	395.82	0.86
15	432.51	263.02	337.28	0.62
23	447.71	324.24	381.01	0.80
26	459.90	253.51	341.45	0.64
27	399.94	291.07	341.19	0.64
28	427.56	299.23	357.69	0.70
31	423.64	214.78	301.64	0.50
32	392.64	345.94	368.55	0.75
45	377.57	263.03	315.14	0.55
46	479.73	349.14	409.26	0.92
51	440.55	319.89	375.40	0.77
58	425.60	304.09	359.75	0.71
62	399.02	293.76	342.37	0.64
68	456.03	375.84	414.00	0.94
86	389.94	321.37	354.00	0.69
93	500.03	311.89	394.91	0.86
94	456.03	261.82	345.54	0.66
95	508.16	381.07	440.05	1.06
102	374.97	283.79	326.21	0.58
143	488.65	308.32	388.15	0.83
145	407.38	327.34	365.17	0.73
159	415.91	261.22	329.61	0.60
163	374.97	353.99	364.33	0.73
182	410.20	341.98	374.54	0.77
183	413.05	351.56	381.07	0.80
184	463.45	282.49	361.83	0.72
195	402.72	247.17	315.50	0.55
Zagross	404.58	281.19	337.29	0.62
Norstar	349.95	273.53	309.39	0.53
Mean	426.75	303.92	359.20	0.71

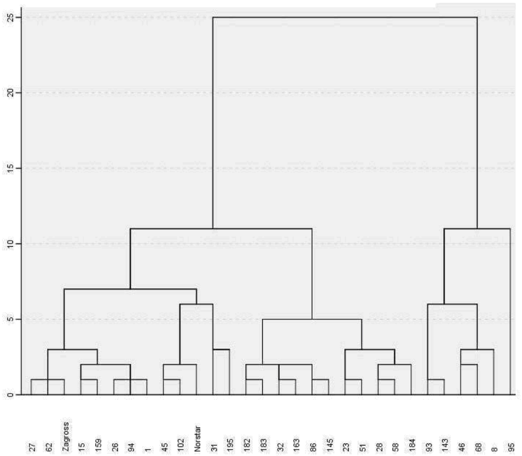

Fig. 1. Cluster analysis of recombinant inbred lines of wheat together with their parents (Norstar and Zagross) based on grain yield in the normal and water stress conditions, STI, and GMP using the average linkage algorithm and Euclidean distance measure.

Conclusion

Evaluation of 28 recombinant inbred lines of wheat developed from the cross of Norstar and Zagross varieties at normal and water stress conditions over two years showed significant genetic variation and genotype by environment interaction for all traits. Moderate genetic gain for most of the characters indicated the possibility of selection among the lines under study. Transgressive segregation for grain yield at normal and water stress environments and also for GMP and STI indices was observed among the recombinant inbred lines under investigation. Six promising lines for drought tolerance were identified in the cluster analysis and recommended for further evaluation in different environmental conditions.

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