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Evaluation of genetic diversity and QTLs controlling drought tolerance indicators in agropyron using wheat-agropyron disomic addition lines

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Abstract

In order to study genetic diversity and locating QTLs controlling indicators of drought tolerance, disomic chromosome addition lines of *Agropyron elongatum* (donor) into the genetic background of Chinese Spring (recipient) were tested in the field under irrigated and rainfed conditions. Analysis of variance exhibited significant differences for stress yield (Ys), seed per plant (SPP), seed per spike (SPS), seed weight (SW), relative water content (RWC) and leaf water potential (LWP) indicating the presence of genetic variability and possible chromosomal localization of QTLs monitoring agro-physiological criteria of drought tolerance in *Agropyron*. Comparison of means showed that the disomic addition lines 3E, 5E, 5E, 6E, 7E and 3E had the highest Ys, SPP, SPS, SW, RWC and LWP respectively, while chromosome 2E revealed the lowest amount of RWL, therefore QTLs controlling agro-physiological indicators of drought tolerance in *Agropyron* are distributed on chromosomes 2E, 3E, 5E, 6E and 7E among which chromosomes 3E, 5E and 7E were outstanding. The highest amount of stress tolerance index (STI), geometric mean productivity (GMP), harmonic mean (HM) and yield index (YI) was attributed to addition lines 4E and 5E, therefore QTLs monitoring yield based drought tolerance indicators are located on chromosomes 4E and 5E and hence they can be used for improvement of drought tolerance in wheat through chromosome engineering. High broad sense heritability was observed for all characters except SPP and LWP expressing low genetic potentials, high effect of environment and absence of additive gene action in the inheritance of SPP and LWP.

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Introduction

Bread wheat (*Triticum aestivum* L.) is a major food grain in Iran, therefore improving yield and yield stability is the primary objective of wheat breeding programs in this country (Ram *et al.*, 2007).

Drought is a major constraint in wheat production and the most important contributor to yield reduction in semiarid regions. Breeding drought-resistant cultivars is, therefore, a major objective in plant breeding programmes for rainfed agriculture in these regions (Ehdaie and Waines, 1993; Andrew *et al.*, 2000).

Selecting wheat genotypes based on their yield performance under drought conditions is a common approach for improvement of drought tolerance, therefore some drought stress indices or selection criteria which provide a measure of drought based on yield loss under drought conditions in comparison to normal conditions have been used for screening drought tolerant genotypes (Pireivatlou *et al.*, 2010; Mohammadi *et al.*, 2010; Nouri *et al.*, 2011).

Breeding for drought tolerance by selecting solely for grain yield is difficult because the heritability of yield under drought conditions is low, due to small genotypic variance or to the large genotype – environment interaction variances (Ludlow and Muchow, 1990; Kőszegi *et al.*, 1996). Therefore evaluation of some of the physiological traits involved in stress tolerance was proposed (Blum, 1988). The incorporation of such attributes into a potentially high-yielding genotype may improve its adaptability and thus its response to environmental variability (Jaradat, 1991).

Genetic variability is essentially the first step of breeding for crop improvement which is immediately available from germplasm reservoir of variability for different characters (Vavilov, 1951). Since most of the economic characters including yield are polygenically controlled and are much influenced by environmental factors, an understanding of inheritance and study of

association between yield and its components is necessary for planning an effective selection program in identifying high yielding genotypes. However, the inheritance of quantitative characters is often influenced by variation in other characters, which may be due to pleiotropy genetic linkage (Hanson *et al.*, 1956). As grain yield and various morphological and physiological characters contributing to grain yield under drought are greatly influenced by various environmental conditions, therefore it is necessary to separate the total phenotypic variation into heritable and non-heritable components with the help of genetic parameters such as: genotypic and phenotypic coefficients of variation, heritability, coheritability and genetic gain, degree of association between the various characters, direct and indirect effects of characters contributing to total yield are of permanent significance in formulating appropriate breeding strategy and exploiting the inherent variability of the experimental materials (Ali *et al.*, 2009; Kahrizi *et al.*, 2010).

Species related to wheat, including both distantly related and progenitor species, represent a large reservoir of useful variability that can be exploited in wheat improvement (Jiang *et al.*, 1994; Friebe *et al.*, 1996). They contain indispensable genes required for wheat improvement especially under an unfavourable environment. They generally have tolerance to biotic and abiotic stresses and survive under low input conditions. Not much work has been done on the transfer of quantitative traits such as drought, cold and salinity tolerance. This is mainly because of the fact that these traits are mainly governed by minor genes with small effects (QTLs). Because of the complex nature of drought tolerance, little information is available on the chromosomal location of the genes conditioning drought tolerance and related physiological traits affecting drought tolerance (Farshadfar, 1995).

Disomic alien addition lines (DAALs), in which single pairs of homologous chromosomes from a related species are added to the wheat complement, are

worthwhile material to identify alien chromosomes carrying useful genes and form the starting point for the cytogenetic transfer of alien genetic material to wheat (Szakács and Molnár-Láng, 2010).

The present investigation was carried out (i) to locate QTLs controlling agro-physiological predictors of drought tolerance (ii) to estimate genetic parameters and genetic diversity of the characters studied and (iii) to study association between the traits and yield under raifed conditions.

Material and methods

Plant genetic materials

To locate QTLs controlling agro-physiological predictors of drought tolerance and estimation of genetic parameters in *Agropyron*, a set of 8 disomic chromosome addition lines (1E to 7E) of *Agropyron elongatum* (2n=2x=14) (Donor) into the genetic background of Chinese Spring (CS) wheat (2n=6x=42) (Recipient) were tested in the field (Table 1). The genetic materials were evaluated under rainfed condition for one year at Research field of Campus of Agriculture and Natural Resources of Razi University, Kermanshah, Iran, during 2012-2013 growing season. The experimental design was a completely randomized block design with three replications. The plots consisted of 2m and at 15×25 cm inter-plant and inter-row distances, respectively. Each plot consisted of 100 seeds (each row 50 seeds). At the time of harvesting 5 single plants were selected randomly and grain yield was determined. The following agro-physiological characters were also measured:

Table 1. Disomic addition lines and Chinese Spring (CS).

Codes	Genome	Chromosomes
1	1E	44
2	2E	44
3	3E	44
4	4E	44
5	5E	44
6	6E	44
7	7E	44
8	CS	42

Agronomic and yield based criteria

Grain yield under stress (Ys) and irrigated (Yp) conditions, yield components (number of seed per spike = SPS, number of spike per plant = SPP and 1000- seed weight = SW), for each treatment at each replicate were measured. Drought tolerance indices were calculated based on grain yield per plot for stress (Ys), non-stress (Yp) and total mean of grain yield for stress (\bar{Y}_s) and non-stress (\bar{Y}_p) conditions as follows:

Stress tolerance index (STI) and geometric mean productivity (GMP) (Fernandez, 1992):

$$STI = (Y_p \times Y_s) / (\bar{Y}_p)^2$$

$$GMP = \sqrt{(Y_s \times Y_p)}$$

Yield index (YI) = $Y_s / (\bar{Y}_s)$ (Gavuzzi *et al.*, 1997)

Harmonic mean (HM) = $2 (Y_p \times Y_s) / (Y_p + Y_s)$ (Farshadfar *et al.*, 2013)

Physiologic characters

Relative water content (RWC)

Five flag leaves (0.5 g) were taken and weighed for fresh weight (FW). Then, segments were placed in distilled water for 24 h and reweighed to obtain turgor weight (TW). Thereafter the leaf segments were oven dried for 48 h in 72°C and weighed (dried weight, DW). RWC was calculated using the following formula (Eric *et al.*, 2005):

$$RWC(\%) = \left[\frac{FW - DW}{TW - DW} \right] \times 100$$

Relative water loss (RWL)

A sample of five flag leaves were taken from each genotype and fresh weight was measured (FW). The leaves were then wilted at 35°C for 5 h and reweighed (W5H). Then the samples were oven dried for 70°C and weighed again (DW). RWL was calculated by the following formula (Farshadfar *et al.*, 2000):

$$RWL = \frac{FW - W5H}{FW - DW} \times 100$$

Leaf water potential (LWP)

LWP was measured on flag leaves of each replication using a pressure chamber (Model PMS Instrument Co.)

Biometrical genetic analysis

The recorded data were subjected to analysis of variance using SAS V9.1 software to ascertain existence of variability among the genotypes. The phenotypic and genotypic coefficient of variation (PCV and GCV), broad sense heritability (h^2_{bs}), genetic gain and co-heritability were estimated according to (Farshadfar, 2010) from the components of variance and covariance as follows:

$$V_E = MSE,$$

$$V_G = (MSg - MSE)/r$$

$$V_P = V_G + V_E$$

$$PCV = 100 \sqrt{\sigma_p^2 / \bar{x}}$$

$$GCV = 100 \sqrt{\sigma_g^2 / \bar{x}}$$

$$ECV = 100 \sqrt{\sigma_e^2 / \bar{x}}$$

$$h^2_{bs} = \sigma_g^2 / \sigma_p^2$$

$$GG = (i \cdot \sigma_g^2 / \sqrt{\sigma_p^2}) 100 / \bar{x}$$

$$E(MSP_V) = \sigma_{e_1e_2} + r \sigma_{g_1g_2}$$

$$E(MSP_e) = \sigma_{e_1e_2}$$

$$\sigma_{g_1g_2} = (MSP_V - MSP_e) / r$$

$$\sigma_{p_1p_2} = \sigma_{g_1g_2} + \sigma_{e_1e_2}$$

$$SI = K \times (V_p)^{0.5}$$

Where, V_e = environmental variation, MSE = error mean square, V_g = genotypic variation, r = number of replication, V_p = phenotypic variation \bar{x} is the mean, σ_g^2 is genetic variance, σ_p^2 is phenotypic variance, PCV = phenotypic coefficient of variation, GCV = genotypic coefficient of variation, ECV = environmental coefficient of variation, h^2_{bs} = broadsense heritability, GG = genetec gain, the standard selection differential (i) for 5% selection

intensity was 2.06, $\sigma^2_{g(1,2)}$ = genetic covariance of characters 1 and 2, $\sigma^2_{p(1,2)}$ is phenotypic covariance for characters 1 and 2, $\sigma_{e_1e_2}$ = environment covariance of character 1 and 2, SI = value of selection index for each character and $K = 2.06$ at 5% selection intensity (Kang *et al.*, 1983).

Efficiency of the added chromosome (EAC): The EAC for each line was calculated (Farshadfar *et al.*, 2003) as:

$$EAC = [(Character\ of\ addition\ line - Character\ of\ CS) / Character\ of\ CS] \times 10$$

Results and discussion

Analysis of variance and comparison of means

Analysis of variance exhibited significant differences for SPP, SPS, SW, RWC and LWP (Table 2) indicating the presence of genetic variability and possible chromosomal localization of QTLs monitoring agro-physiological criteria of drought tolerance in *Agropyron*. No significant difference was found between the addition lines for Ys and RWC, but as F-test in the analysis of variance can only detect large differences between the genotypes, therefore non-significancy in the table of analysis of variance does not mean no significant difference between addition lines for the characters Ys and RWC, that is why mean comparisons classified these traits in different groups (Bassiri, 1990). Several researchers reported phenotypic divergence and extensive variation for RWC in wheat (Kashif and Khaliq, 2004), in barley (Martin *et al.*, 1989) and in wild relatives of wheat (Farooq *et al.*, 2002).

Table 2. Analysis of variance for various characters investigated.

SOV	df	Ys	SPP	SPS	SW	RWC	RWL	LWP
Rep.	2	0.887	8.375	43.565	8.417	1.396	0.002	9.042**
Gen.	7	1.948 ^{ns}	9.714**	355.790**	102.082**	58.607**	0.016 ^{ns}	51.137**
Error	14	0.200	2.946	38.825	10.356	4.633	0.001	17.280
CV%		22.63	22.89	22.93	20.66	3.05	20.10	13.95

**Significant at 1% level of probability, *Significant at 5% level of probability

Comparison of means (Table 3) showed that the disomic addition lines 3E, 5E, 5E, 6E, 7E and 3E had the highest Ys, SPP, SPS, SW, RWC and LWP respectively, while chromosome 2E revealed the lowest amount of RWL, therefore QTLs controlling agro-physiological indicators of drought tolerance in *Agropyron* are distributed on chromosomes 2E, 3E, 4E, 5E, 6E and 7E among which chromosomes 3E, 5E and 7E are outstanding. Farshadfar *et al.* (2002) showed that most of the QTLs controlling drought

tolerance criteria in *Agropyron* are located on chromosomes 3E, 5E and 7E, which collectively constitute 84.3% of the additive genetic variance. Farshadfar (2011) also reported that QTLs monitoring genotype × environment interactions in *Agropyron* are located on chromosome 7E. The importance of chromosomes 3E (Dvorak, 1993) and 5E (Mahmood and Quarrie, 1993) were also investigated for salt tolerance.

Table 3. Mean comparisons of agro-physiological characteristics of dsomic addition lines.

Gen	Ys	SPP	SPS	SW	RWC	RWL	LWP
1	1.67bc	5.67b	23.63c	13.17bc	69.23cd	0.19bc	34.67a
2	2.02abc	5.67b	24.73c	15.07bc	66.93cd	0.12d	32.00ab
3	2.84a	9.00a	29.77bc	16.04b	65.57d	0.17cd	35.00a
4	1.26cd	9.00a	26.50c	9.53c	69.80c	0.16cd	29.00abc
5	2.19ab	9.33a	38.43ab	9.60c	69.05cd	0.24b	26.33bc
6	0.50d	5.67b	5.72d	25.17a	70.90bc	0.15cd	31.00abc
7	2.73a	6.33ab	26.67c	23.30a	79.53a	0.34a	23.33c
8	2.60a	9.33a	41.92a	12.73bc	74.23b	0.15cd	27.00abc
LSD 5%	0.783	3.006	10.91	5.636	3.769	0.055	7.280
Min	0.50	5.67	5.72	9.53	65.57	0.12	23.33
Max	2.84	9.33	41.92	25.17	79.53	0.34	35.00

The genotypes 4E and 5E disomic additional lines had the highest drought resistance based on STI, GMP, HM and YI (Table 4), therefore genes controlling

drought resistance and high grain yield in both stress and nonstress conditions are located on chromosomes 4E and 5E.

Table 4. Yield based drought tolerance indices in wheat-agropyron disomic addition lines.

Genotypes	Yp	Ys	GMP	HM	YI	STI
1E	11.033(1)	2.222(4)	4.951(4)	3.699(4)	0.750(4)	3.290(4)
2E	9.767(2)	2.775(3)	5.206(2)	4.322(3)	0.936(3)	3.637(2)
3E	6.876(5)	1.903(7)	3.618(6)	2.981(6)	0.642(7)	1.757(6)
4E	7.336(4)	6.026(1)	6.649(1)	6.617(1)	2.033(1)	5.933(1)
5E	5.182(7)	4.917(2)	5.048(3)	5.046(2)	1.659(2)	3.420(3)
6E	6.325(6)	2.212(5)	3.741(5)	3.278(5)	0.746(5)	1.878(5)
7E	5.156(8)	2.083(6)	3.277(8)	2.967(7)	0.703(6)	1.441(8)
CS	7.934(3)	1.572(8)	3.532(7)	2.624(8)	0.530(8)	1.674(7)

Efficiency of added chromosomes (EAC)

Efficiency of added chromosomes (Table 5) showed that maximum EAC for the characters Ys, SW, RWC, RWL and LWP belonged to chromosomes 3E, 6E, 7E, (1E and 7E) and 3E. The efficiency of added chromosomes in wheat-barley disomic addition lines

under drought condition was attributed to chromosomes 4H and 5H (Vaisi and Farshadfar, 2011) and in wheat-rye disomic addition lines was related to chromosomes 3R and 7R (Farshadfar *et al.*, 2003) with positive effect and enhancement of drought tolerance.

Table 5. Efficiency of added chromosomes for the characters investigated.

Genotypes	EAC _{gy}	EAC _{SPP}	EAC _{SPS}	EAC _{SW}	EAC _{RWC}	EAC _{RWL}	EAC _{LWP}
1E	-0.3576	-0.3922	-0.4363	0.0345	-0.0673	0.2666	0.2212
2E	-0.2230	-0.3922	-0.4100	0.1838	-0.0983	-0.2	0.1851
3E	0.0923	-0.0353	-0.2898	0.2600	-0.1166	0.1333	0.2962
4E	-0.5153	-0.0353	-0.3678	-0.2513	-0.0596	0.0666	0.0740
5E	-0.1576	0	-0.0832	-0.2458	-0.0697	0.6	-0.0248
6E	-0.8076	-0.3922	-0.8635	0.9772	-0.0448	0	0.1481
7E	0.05	-0.3215	-0.3637	0.8303	0.0713	0.2666	-0.1359

Genetic diversity

Genetic parameters are presented in Table 6. PCV and GCV were low for RWC. On the other hand, GG had the highest amount for SPS. High broad sense heritability estimate was observed for all characters except SPP and LWP indicating low genetic potentials, high effect of environment and absence of additive gene action in the inheritance of SPP and LWP. High broad sense heritability ($h^2_{bs} > 0.5$) (Stanfield, 2005) in the genetic of other criteria is a suitable basis for reliable selection of the characters

investigated (Kandasamy *et al.*, 1989; Thiyagarajan, 1990). Heritability estimates along with genetic gain are very useful in predicting expected gain under selection instead of heritability alone. High heritability estimates with high GG in SPS, SW and RWC indicates that due to additive gene effects direct selection may be effective in the inheritance of these traits (Soomro *et al.*, 2010). RWL showed very low level of GG exhibiting high influence of environmental conditions for their expression under irrigated condition.

Table 6. Estimates of genetic parameters for the investigated traits.

Traits	Mean	σ^2_G	σ^2_P	$cov_{P(GY,i)}$	$cov_{G(GY,i)}$	h^2_{bs}	PCV	GCV	GG	SI
GY	1.98	0.583	0.783	-----	-----	0.74	44.79	38.65	1.36	1.60
SPP	7.50	2.2565	5.202	0.665	0.537	0.43	30.41	20.03	2.04	10.70
SPS	27.17	105.653	144.478	7.253	6.344	0.73	44.19	37.79	18.11	297.6
SW	15.58	30.574	40.931	-0.566	-0.981	0.75	41.01	35.45	9.84	84.30
RWC	70.66	17.979	22.624	0.875	0.569	0.80	6.73	6.00	7.79	46.60
RWL	0.19	0.0047	.0061	0.021	0.023	0.83	40.77	37.22	0.13	0.013
LWP	29.79	11.282	28.565	-0.800	-0.758	0.39	17.84	11.11	4.27	58.80

Comstock and Moll (1963) reported that more diverse the environmental population the smaller the estimates of genetic variance which supports the present result of low estimates of GG for RWL. Low heritability estimates also explained the presence of non-allelic interaction in the inheritance of SPP and LWP.

effective than dominance and dominance \times dominance effects in the genetic of all characters except SPP and LWP. High heritable characters were least affected by environmental fluctuations, hence simple selection method would be effective for improvement of these traits under water shortage condition.

Considering the broadsense heritability estimates, all the traits except SPP and LWP were ranked as high heritable suggesting that the parents used to develop addition lines in early generations were desirable. The high heritability estimates also revealed that the additive and additive \times additive effect were more

Ys and RWL showed high heritability estimates with low GG, while LWP exhibited low heritability but higher GG. Higher broad-sense heritability estimates do not necessarily provide high values of genetic gain, therefore heritability alone provides no indication of genetic progress for the trait under selection (Ansari

et al., 2002; Hussain *et al.*, 1999; Larik *et al.*, 1997). High heritability associated with low GG for Ys and RWL was probably due to non-additive gene action (dominance and epistasis) (Sharma and Tyagi, 1990, 1991) and the presence of genotype × environment interaction. In such cases simple selection may not be rewarding (Kumar *et al.*, 2002) and breeders can select desirable transgressive segregants.

A successful breeding method will be the one exploiting the non-additive gene effects. The methods which mop-up the non-additive effects are restricted recurrent selection by the way of intermating the most desirable segregants followed by selection (Joshi, 1979) and a diallel selective mating (Jensen, 1978).

The knowledge of the genotypic and phenotypic variances for each parameter is necessary to construct a definite selection index (Sprague, 1966). Considering the value of SI (Table 6) maximum SI was attributed to SPS and SW and minimum to RWL and HI, respectively.

Phenotypic and Genotypic matrices

The most common way to represent the pattern and magnitude of the genetic basis of a series of traits is the genetic variance – covariance matrix, also known as the G-matrix. G-matrix is extremely useful for predicting the response to selection and improvement

of the efficiency of selection over a short period. As G-matrix includes genetic covariance as well, it can also help to predict the indirect response to selection of one character from selection on another trait. If the genetic covariance between two traits is different from zero, selection on one trait will affect response to selection on the other (Guillaume and Whitlock, 2007; Kearsy and Pooni, 2004). Genetic covariances between traits can occur because of linkage/linkage disequilibrium and pleiotropy (Kearsy and Pooni, 2004). According to the results (Table 7), the highest genetic covariance observed between SPS and SW, LWP and between SW and RWC and between RWC and LWP, respectively. Also these results showed that (Table 7), the highest phenotypic covariance observed between SPS, SPP and Ys; between SW, SPP and SPS and between LWP, SPS and RWC respectively. High values of genetic and/or phenotypic covariance between two traits may represent a high level of variation (genetic, phenotypic or both) between two traits. Also the results suggested that selection for low quantity of SW and LWP and high value of SPS will increase Ys indirectly (correlated response). Much of the covariation in small populations is due to correlated gene frequencies and loose linkages which are transient. They can normally be removed by random mating and keeping the population size large. Tight linkages and certain types of pleiotropy, on the other hand are difficult to manipulate (Kearsy and Pooni, 2004).

Table 7. Phenotypic (Lower off-diagonal matrix) and Genotypic (Upper off-diagonal matrix) covariance matrix.

	GY	SPP	SPS	SW	RWC	RWL	LWP
GY							
SPP	0.665						
SPS	7.253	19.710					
SW	-0.566	-9.078	-49.047				
RWC	0.875	-2.153	2.449	14.053			
RWL	0.021	-0.017	0.054	0.147	0.234		
LWP	-0.800	1.327	-11.598	-8.569	-19.29	-0.217	

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