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Genetic Study of Grain Yield and its Components in Bread Wheat Using Generation Mean Analysis under Water Stress Condition

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Abstract

In order to study the inheritance of grain yield and its components in bread wheat, two cultivars, Karchyya(drought and salinity tolerant) and Gaspard (sensitive to drought and salinity stress) were crossed.Parents together with F1, F2, F3, BC1and BC2 generations were evaluated using a randomized complete block design with three replications in 2008-2009 growing season.Grain weight per spike, number of grains per spike, 1000 grain weight, number of spikes per plant and grain yield per plant were recorded. Analysis of variance indicated significant differencesamong generationsforall traits. Mid-parent heterosis for number of grains per spike and high-parent heterosisfor rest of the traits indicated the role of dominance gene action in governing the studied characters. Furthermore, estimates of degree of dominance was in the over-dominance range for all traits. Based onthe generation mean analysis and the subsequent joint scaling test,additive-dominance model wasinsufficient for explaining the inheritance of the agronomic characters under study. Therefore, different models consisting of four to six parameterswere fitted to the generation means.Considering all traits, at least one epistaticeffect was significant in the fitted models.These results suggest the importance of non-additive gene action in controlling the grain yield and its components in the terminal water stress condition. Therefore, breeding programs utilizing this type of gene action are recommended if hybridization problems could be solved in this important crop. The broad-sense and narrow-sense heritability of the traits were estimated from 0.31 to 0.42 and from 0.10 to 0.42, respectively. The narrow-sense heritability of 1000 grain weight and number of grains per spike were higher than that of grain yield per plant. This suggests that selection for grain yield in segregating generations would not be as effective as the yield components such as 1000 grain weight and number of grains per spike.

Keywords: Bread wheat; Gene action; Generation mean analysis; Generation variances; Heritability

Introduction

Grain yield is a complexcharacter and selection for this trait during segregating generations may not be effectivedue to large genotype by environment interaction. Thus, the use of some yield componentswhich have higher heritability than the grain yield and correlate well with this character is justifiable for the individual-plant and family selection during the earlysegregating generations (Sharma1998). In this regard, the knowledge about geneticparameters of the yield componentscould help breeders to adopt an appropriate breeding system to improve the grain yield. Generation mean analysis is one of the methodsthat provide information about the genetic effects governing the traits under study (Mather and Jinks 1982). Jinks and Pooni (1979) stated that the type of gene action is important in choosing the breeding strategy. Baghizadeh*et al*. (2004) used generation mean analysis in barley and showed that non-additive effectswere responsible in governing number of spikes, grain yield per plant and plant biomass. Prakash*et al.* (2006) found that the dominance effectstogether with additive effects, additive × dominance interaction and additive × additive interaction, had a role in controlling the traits of wheat under investigation. Ahmady*et al.* (2007) by the use of generation mean analysis studied the inheritance of grain yield, plant height, plant weight, spike length and 1000 grain weight in wheat and concluded that the dominance effect was the most important factor in controllingthe genetics of these traits.

Effect of water stress condition on grain yield at the reproductive stage is more important than the vegetative stage (Fischer and Maurer 1978).Based on Fischer and Maurer (1978) the decrease in the grain yield ranged from 27%to 86% in the terminal water stress condition. Theobjectives of this research program was to investigate the type of gene action governing yield and its components in bread wheat using generation mean analysis and also to estimate broad-sense and narrow-sense heritability of the studied traits under terminal water stress condition.

Materials and Methods

In order to carry out a generation mean analysis, two wheat cultivars (Karchyya, tolerantto drought and salinity and Gaspard, sensitive to drought and salinity) were crossedto produceF1, F2, F3, BC1 and BC2 generations over three years. These generations,together with the parental cultivars,were evaluated in the Torogh Agricultural Research Station, Mashhad, Iran, during the 2008-2009 growing season using a randomized complete block design with three replicationsunder terminal water stress condition (irrigation withheld in the heading stage). The experimental sitewas located in south-east of Mashhad(with a distance of six kilometers),Iran, with the latitude of 36°13' North, longitude of 59°40'East andthe altitude of 985 meters above the sea level. The following datawere reported in the site: maximum temperature of 43.4ºC, minimum temperature of -27.8 ºC and annual rainfall of 256 millimeters.Mashhad is regarded asa cold and dryarea.Numbers of evaluated plants per plot varied according to the type of generation: 15 plants for P1, P2 and F1 generations, 250, 60 and 70 plants for F2, BC1 and BC2 generations, respectively and 15 plants for eachof 100 F3families. Grain weight per spike, grain number per spike, 1000 grain weight, number of spikes per plant and grain yield per plantwere measured during the growing season.

Generation mean analysis via weighted least squares method,using the inverse of variance within each generation as the weight, was performedfor the models having 2 to 6 parameters. The 6-parameter model is shown below:

$Y=m+\alpha[a]+\beta[d]+\alpha^2[aa]+2\alpha\beta[ad]+\beta^2[dd]$

where,Y=the observed generationmean, m= the mean of all possible inbreds after ∞selfing); [*a*]=additive effect; [*d*]=dominance effect, [*aa*]=additive × additive epistasis,[ad]=additive × dominanceepistasis and [*dd*]= dominance × dominance epistasis(Falconer1996). In order to select the best fitted model for each character, a joint scaling test was performedusing χ^2 test statistics (Mather and Jinks 1982).

Broad-sense heritability (h^2_{BS}) was calculated usingfive different methods of estimating the environmental variance:

1) $[V_{F2} - (V_{P1} + V_{P2})/2]/V_{F2}$ (Allard 1960)
2) $[V_{F2} - (V_{P1} \times V_{P2})^{1/2}]/V_{F2}$ (Mahmud and Kramer 1951)
3) $[V_{F2} - (V_{P1} \times V_{P2} \times V_{F1})^{1/3}]/V_{F2}$ (Warner 1952)
4) $[V_{F2} - (V_{P1} + V_{P2} + V_{F1})/3]/V_{F2}$ (Allard 1960)
5) $[V_{F2} - (V_{P1} + V_{P2} + 2V_{F1})/4]/V_{F2}$ (Mather and Jinks 1982)

In addition, narrow-sense heritability (h^2_{NS}), which is important in breeding programs, wasestimatedby the following formula(Warner 1952):

$h^2_{NS=}$ $[2V_{F2} - (V_{BC1} + V_{BC2})]/V_{F2}$

In the above formulae,V_{P1}=Variance within the first parent,V_{P2}=Variance within the second parent,$V_{F1=}$ Variance among F1individuals, V_{F2}= Variance among F2individuals,V_{BC1}=Variance among BC1individuals and V_{BC2}=Variance among BC2individuals.

Furthermore, degree of dominance was calculated as below, based on the additive (D) and dominance (H) variance components estimated from the within-generation variances (Hallauer*et al.*2010).

Degree of dominance= $(H/D)^{1/2}$

Results and Discussion

Analyses of variance and consequent mean comparisons by Duncan multiple range method showed significant differencesamong generations for all agronomic traits under study (Tables 1 and 2).This allowed the possibility of carrying out generation mean analysis for these characters. Karchyya (P1parent),a drought and salinity tolerant cultivarhad higher number of grains per spike,grain weight per spike and grain yield per plantthan Gaspard (P2 parent), a sensitive cultivar to drought and salinity stress under terminal drought stress condition. However, Gaspardwas superior to Karchyyain terms of 1000 grain weight and number of spikes per plant (Table 2). This suggests that different components contribute to grain yield in different cultivars High-parent heterosis was observed for grain yield per plant,grain weight per spike, 1000 grain weight and number of spikes per plant.On the other hand, a mid-parent heterosis was obtained for number of grains per spike.These results indicated the role of dominance gene action in governing the studied characters under the terminal drought stress environment, Generation mean analysis for the traits under study was carried out using a three-parameter model (additive-dominance model).

Table 1.Meansquares for different traits in generations of crosses between two bread wheat cultivars

Sources of variation	Degrees of freedom	Number of grains per spike	Grain weight per spike	1000 grain weight	Number of spikes per plant	Grain yield per plant
Replication	2	16.38^{**}	18.65^{**}	112.22^{**}	17.65^{**}	3.34^{*}
Treatment	105	11.24^{**}	7.19^{**}	10.90^{**}	10.50^{**}	6.92^{**}
Error	210	0.99	0.99	0.93	1	0.99

*,** Significant at 5% and 1%, probability levels, respectively

Table 2.Generation means for different traits in the cross of two bread wheat cultivars

Generation	Number of grains per spike	Grain weight per spike (gr)	1000 grain weight (gr)	Number of spikes per plant	Grain yield per plant (gr)
P1	64.48±1.22a	2.88±0.07ab	44.82±0.64c	11.47±0.55b	23.22±1.39bcd
P2	53.98±1.25b	2.58±0.07c	47.84±0.70b	13.46±0.79ab	20.17±1.92d
F1	56.45±1.53b	2.99±0.09a	53±0.81a	14.25±1.08a	36.87±3.10a
F2	55.60±0.91b	2.64±0.05bc	47.10±0.50bc	13.63±0.52ab	20.39±1.43b
F3	55.84±0.23b	2.61±0.01bc	46.85±0.13bc	15.10±0.12a	28.26±0.31bc
BC1	64.08±1.83a	2.96±0.11a	45.81±0.94bc	12.84±0.94ab	21.7±2.60cd
BC2	56.81±1.39b	2.75±0.08abc	48.44±0.79b	14.69±0.85a	27.14±2.39bc

In each column, means with at least one letter in commonare not significantly different at1% probability level

However, thechi-square was significant for all traitswhich suggest thatthe additive-dominance modelwas not adequate to explain the generation means. Thenall possible four to six-parameter models which included epistatic effects were fitted to the generation means. The best models with non-significantchi-square are presented in Table 3. Additive by additive epistatic effect was present in all traits except 1000 grain weight. A dominance by dominance interaction was also present for grain yield per plantand 1000grain weight. These results indicate the presence of espitatic gene action in governing the agronomic characters in wheat. Panhank*and* Sharma (1983) also showed that epistasis of genes is involved in controlling yield and yield components in wheat. Additive effectwas significant for all yield components showing the importance of additive effects and the possibility of improving these traits through selection in preliminary generations. However, dominance effects and dominanceby dominance interactions were also present for some traits suggesting the need for hybrid production in wheat if breeders can overcome the hybridization barriers. On the other hand, no significant additive×dominance interaction was observed among the traits. The opposite sign between dominance component [d] and the dominance × dominance interaction [dd] indicates the existence of duplicate epistasis which reduces the variance of segregating generations. In general duplicate epistasis can lead to unpredictable results and on the other hand complementary epistasis is important inthe breeding programs(Yadava and Narsinghani 1999). Although the additive component was significant for majority of the characters, but total dominance effects ([d] + [dd]) were larger than total additive effects ([a] + [aa]) explaining again the importance of dominance effects in controlling the genetic variation of the yield and yield components. This indicates that final selection must be made in more advanced generations as well (Matherand Jinks 1982). Baghizadeh *et al* .(2004) obtained similar result in barley.

Table 3. Estimates of genetic components for different traits in the generations of the cross between two bread wheat cultivars

Trait	m	[a]	[d]	[aa]	[ad]	[dd]	χ^2
Number of grains per spike	53.15±1.35**	5.24±0.87**	13.1±6.58*	6.32±1.50**	2.25±4.86^{ns}	10.05±6.05^{ns}	5.27^{s}
Grain weight per spike	2.49±0.03**	0.15±0.04**	0.46±0.10**	0.25±0.06**	....	....	3.77^{ns}
1000grain weight	47.95±0.73**	-1.51±0.47**	-7.56±3.55*	-1.59±0.82^{ns}	-2.38±2.61^{ns}	12.58±3.24**	0.30^{ns}
Number of spikes per plant	16.54±0.77**	-1.02±0.48*	-6.93±3.83^{ns}	-3.99±0.85**	-1.88±2.72^{ns}	4.50±3.73^{ns}	2.03^{ns}
Grain yield per plant	31.51±2.12**	1.57±1.19^{ns}	-19.07±10.64^{ns}	-9.95±2.30**	13.58±7.44^{ns}	24.75±10.5*	1.27^{ns}

*,**, ^{ns}Significant at 5% and 1%, probability levels and non-significant, respectively

Table 4. Estimates of broad-sense and narrow-sense heritability and genetic gainfor different traits in wheat

Trait	Heritability							Degree of dominance
	Broad sense						Narrow sense	
	1	2	3	4	5	Mean		
Number of grains per spike	0.37	0.37	0.40	0.40	0.42	0.39	0.33	1.3
Grain weight per spike	0.40	0.40	0.36	0.36	0.34	0.37	0.21	1.3
1000 grain weight	0.39	0.39	0.43	0.43	0.45	0.42	0.42	1.3
Number of spikes per plant	0.29	0.29	0.47	0.26	0.25	0.31	0.16	1.4
Grain yield per plant	0.43	0.43	0.34	0.33	0.28	0.36	0.10	1.1

Additive and dominance components of genetic variancewere estimated (assuming no epistasis) using variance of generations (Hallaueret *al.* 2010). Therefore, the variances are biased because epistatic effects were present for the traits under study.Estimates of degree of dominance, narrow sense heritability and broad sense heritability, based on additive and dominance components, are shown in Table 4. The average degree of dominance $(H/D)^{1/2}$for all traits was higher than unity indicating theexistence of over-dominance for some loci which represents the importance of dominance effects in governing the studied characters. Similar results were reported by Baghizadeh *et al.*(2004) in barley.

The range of broad-sense heritability for grain yield and related traits wasfrom0.31to0.42, based on theaverage of estimates obtained from five different formula, and that of narrow-sense heritability from0.10 –0.42. Since our experiment was conducted under terminal water stress condition, the low to medium broad-sense heritability can be attributed to the reduction of genetic variability in the stressedenvironment. Golabadi*et al.* (2005) in durum wheat and

Ceccarelli (1994, 1996) in barley alsoreported that heritability of agronomic traits in high-yielding environments ishigher than low yielding conditions. The narrow sense heritability of agronomic characters in this experiment was low to medium. However, grain yield had lower narrow sense heritability (0.10) than 1000 grain weight (0.42) and number of grains per spike (0.33).This indicates that selection for grain yield in segregating generations would not be as effective as its components.

In conclusion, non-additive genetic effects were present in the cross of Karchyyawith Gaspard, suggesting the exploitation of these effects in breeding programs if hybridization problems were solved in the wheat crop.The existence of non-additive genetic effects also implies that selection in early generations would not be as effective as advanced generations, at least in the population generated from this cross.

Aknowlegment

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