Genetic Characteristics of Grain Yield and its Components in Barley (*Hordeum vulgare* L.) Under Normal and Drought Conditions

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Abstract: Drought stress is a major constraint for barley production and yield stability in rainfed ecosystems. The objective of the study was to generate genetic information, which can help in breeding barley cultivars with improved drought tolerance. An six-parent diallel, involving barley varieties Salemer, Orizont, Rihane, Pfyner, Dana and Hemalaya, was evaluated to determine the genetic parameters contributing to number of tillers, number of grains per spike, 1000-grain weight and grain yield per plant under normal and drought conditions. Furthermore, generation mean and variance analyses was carried out on six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) derived from the cross Salemer × Orizont, Rihane × Pfyner and Dana × Hemalaya to complement the genetic information obtained from the diallel analysis. Diallel, generation mean and variance analyses suggested that both additive and dominance effects were important for most of the traits evaluated, but dominance and non-allelic interaction had a more pronounced effect for number of grains per spike in drought and 1000-grain weight and grain yield in both of environments. The highest heritability was obtained for number of grains per spike in normal condition and number of tillers in both environments, indicating that these traits are controlled by additive effects. Because of low genetic gain and heritability for grain yield compared to other characters, selection based on yield components is recommended.

Key words: Barley · Drought stress · Gene action · Diallel · Generation means.

INTRODUCTION

Barley (*Hordeum vulgare* L.) is a crop with a great adaptation potential in many regions of the world, ranking the forth in terms of planting area only after wheat, rice and maize [1]. Growers can obtain a harvest in areas with low precipitations, mainly because this crop has advantages in aspects such as salt tolerance, drought tolerance, frost tolerance and the early period of development.

Abiotic stress (mainly cold, salinity, heat and water stress) is the principal cause of crop failure world wide, dipping average yields for most major crops by more than 50% [2, 3]. Among the environmental stresses water stress is the second contributor to yield reduction after disease [4, 5]. Water stress may arise as a result of two conditions, either due to excess of water or water deficit. Flooding is an example of excess of water, which primarily results in reduced oxygen supply to the roots. But the more common water stress encountered is the water deficit stress known as the drought stress [6]. Drought is a meteorological term and is commonly defined as a period without significant rainfall. Generally drought stress occurs when the available water in the soil is reduced and atmospheric conditions cause continuous loss of water by transpiration or evaporation. Drought stress tolerance is seen in almost all plants but its extent varies from species to species and even within species [7]. Breeders instinctively look for new sources of variation when attempting to improve plants, but tolerance to drought stress is very complex, due to the intricate of interactions between stress factors and various molecular, biochemical and physiological phenomena affecting plant growth [8, 7].

Several studies in the recent past have identified QTLs for drought tolerance in barley. This *et al.* [9] Noli *et al.* [10], Marquez-Cedillo *et al.* [11], Teulat *et al.* [12, 13], Baum *et al.* [14], Teulat *et al.* [15], Hamam Mohammed [16], Talamè *et al.* [17], Mohammadi *et al.* [18], Guo *et al.* [19] and Inostroza *et al.* [20] reported some QTLs for traits that related to drought tolerance mainly on chromosomes 2, 3, 5, 6 and 7 in barley and its wild relatives.

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Table 1: Barley cultivar genotypes, rowed type and their tolerance status

No.	Cultivar	Row type	Hulled or naked	Tolerance	Origin
1	Salemer	Six	Hulled	Tolerant	Swiss
2	Rihane	Six	Naked	Tolerant	Lebanon
3	Dana	Six	Hulled	Tolerant	Romania
4	Orizont	Six	Hulled	Sensitive	Romania
5	Pfyner	Six	Hulled	Sensitive	Swiss
6	Hemalaya	Six	Naked	Sensitive	China

To develop cultivar, yielding better under drought stress, breeder needs the information about the gene action of the traits related to yield and quality responsible for drought tolerance. In barley, a number of studies regarding gene action of agronomic traits are reported in the literature [21-24], however; only a few studies are conducted under drought stress.

The main objective of the present study was to identify genetic architecture of yield and its components under normal and drought conditions.

MATERIALS AND METHODS

Diallel Analysis: The plant material used in this study (Table 1) were (hand) crossed in a half diallel mating scheme in 2007. The 6 parents and their resulting 15 first filials (F_1s) were grown on November 2008, in a randomized block design with three replicates in field under irrigated and rainfed conditions at Moghan region, Iran. The research station ordination on 101 altitude and $48°,22'$ longitude and $39°,23'$ latitude. Average precipitation was 259.8 mm and average temperature was $14.42°C$. Plots of parents and F_1s consisted of two rows of 1 m length with 20 cm spacing between rows and 5 cm between plants. Ten healthy vigorous plants in the parents and F_1s progenies were selected randomly for recording observations on four characters, namely: number of tillers per plant, number of grains per spike, 1000-grain weight (g) and grain yield per plant (g).

Statistical Analyses: The differences among populations were tested by analysis of variance for individual characters. To fulfill the assumption of absence of epistasis, no multiple allelism and independent gene distribution data was subjected to tests [the uniformity of Wr and Vr test (t^2) and the analysis of regression coefficient test] as described by Singh and Chaudhary [25].

The genetic components of variance, i.e. additive variance (D), variance due to dominant effects of genes (H_1), variance due to dominant effect of genes correlated for gene distribution (H_2), relative frequency of dominant and recessive alleles (F), over dominance effects of heterozygous loci (h^2), environmental variance (E), average degree of dominance $(H_1/D)^{1/2}$, proportion of genes with positive and negative effects in parents ($H_2/4H_1$), proportion of dominant and recessive genes in the parents (K_D/K_R) and heritability both in broad-sense and narrow-sense were estimated using the procedures giving by Jinks and Hayman [26], Hayman [27, 28] and Mather and Jinks [29].

Generation Mean and Variance Analyses: Generation mean analysis was carried out on the six basic generations the P_1 and P_2 (parent cultivars), the F_1 and F_2 (first and second filial generations) and the BC_1 and BC_2 (first and second back crosses) of three combinations of the parental cultivars, Salemer × Orizont, Rihane × Pfyner and Dana × Hemalaya to complement the genetic information from the diallel analysis. We used the parents of the respective crosses as the male parent and the F_1 generation as the female parent and effect back crosses to produce the BC_1 (F_1 back crossed to P_1) and BC_2 (F_1 back crossed to P_2) generations and the F_1 hybrids were selfed to obtain F_2 seeds. All these generations were produced during two cropping seasons and, as such, all the six generations had to be grown together during the same cropping season (2008-2009) in a randomized block design with three replications in field under irrigated and rainfed conditions at Moghan region. In each replication there were two rows for each of the parents and F_1, 7 rows for each of the F_2 and 5 rows for each backcross generation. The length of row was 1 m. Row to row and plant-to-plant distance was 20 and 5 cm, respectively. At maturity 10 guarded plants from each of the parents and F_1, 15 plants from each of the backcross populations and 60 plants from each of the F_2 populations were selected at random to record the data on individual plant basis.

Statistical Analysis: Data were subjected to analysis of variance according to Steel *et al.* [30] to find significant differences among generations for the recorded data.

Generation mean analysis was performed using the Mather and Jinks method [29]. In this method, mean of each character is expressed as follows:

$$Y = m + \alpha[d] + \beta[h] + \alpha^2[i] + 2\alpha\beta[j] + \beta^2[l]$$

Where:

Y : Mean of one generation
m : Mean of all generations
[d] : Sum of additive effects
[h] : Sum of dominance effects
[i] : Sum of additive × additive interaction
[j] : Sum of additive × dominance interaction
[l] : Sum of dominance × dominance Interaction and α, β, α^2, $2\alpha\beta$ and β^2 are the coefficients of genetic parameters. The genetic model that best fits the data was found by the mean of joint scaling test [29] and the accuracy of the models was verified by chi-square (χ^2) test. Components within each model were evaluated for significance by t-test. The type of epistasis was determined only when dominance [h] and dominance × dominance [l] effects were significant. When these effects had the same sign, the effects were complementary while different signs indicated duplicate epistasis [31]. Variance components (additive, dominance and environmental) were estimated as described by Kearsey and Pooni [31], using the following equations:

$$D = 4VF_2 - 2(VBC_1 + VBC_2)$$
$$H = 4(VBC_1 + VBC_2 - VF_2 - Ew)$$
$$F = VBC_1 - VBC_2$$
$$Ew = (VP_1 + VP_2 + 2VF_1)/4$$

Where:

D : Additive variance
H : Dominance variance
F : Correlation between D and H over all loci
Ew : Environmental component of variance

Broad-sense and narrow-sense heritabilities values calculated using the following formula:

$$h_{bS}^2 = \{[VF_2 - (VP_1 + VP_2 + 2VF_1)/4]/VF_2\} \qquad [29]$$

$$h_{bS}^2 = \{[VF_2 - (VP_1 \times VP_2)^{1/2}]/VF_2\} \qquad [32]$$

$$h_{bS}^2 = \{[VF_2 - (VP_1 + VP_2 + VF_1)/3]/VF_2\} \qquad [33]$$

$$h_{bS}^2 = \{[VF_2 - (VP_1 \times VP_2 \times VF_1)^{1/3}]/VF_2\} \qquad [34]$$

$$h_{bS}^2 = \{[VF_2 - (VP_1 + VP_2)/2]/VF_2\} \qquad [33]$$

$$h_{nS}^2 = \{[VF_2 - (VBC_1 + VBC_2)/2]/VF_2\} \qquad [34]$$

Response to selection was estimated with 5% selection intensity (i) (selection differential, K= 2.06) as:

$$Gs = i \times h_{nS}^2 \times \sqrt{VF_2}$$

RESULTS

Diallel Analysis: The differences among the genotypes (parents and F_1's of cross combinations) were highly significant for all the traits in both conditions (data not shown). Genetic components of variation (Table 2) indicated both additive and dominant gene actions for number of tillers and number of grains per spike in stress condition and 1000-grain weight in both conditions, whereas only additive gene action for number of tillers and number of grains per spike in non-stress environment. Also the two measures of dominance (H_1 and H_2) were highly significant for grain yield per plant in both conditions.

Average degree of dominance indicated partial dominance for number of tillers and number of grains per spike in both environments, while over dominance for 1000-grain weight in non-stress condition and grain yield per plant in both conditions. However this ratio indicated complete dominance for 1000-grain weight in rainfed condition. Also, high broad-sense and narrow-sense heritabilities for number of grains per spike in normal and number of tillers in both environments indicated that the greater proportions of the heritable variation of these traits were of additive nature.

The H_1 and H_2 values were different for number of tillers and grain yield in irrigated and 1000-grain weight in both conditions suggesting the asymmetry of positive and negative gene distribution (Table 2). However, H_1 and H_2 values were almost equal for grain yield and number of tillers in rainfed condition and number of grains per spike in both environments, suggesting the symmetry of positive and negative gene distribution. These results were supported by $H_2/4H_1$ ratios, which shower lower ratio than 0.25 for grain yield and number of tillers in normal condition and 1000-grain weight in both conditions while the $H_2/4H_1$ ratio was almost equal to 0.25 for grain yield and number of tillers in stress and number of grains per spike in both conditions. The F component was negative but non-significant for number of tillers, number of grains per spike and 1000-grain weight in normal and grain yield

Table 2: Components of diallel variance and their estimates of various traits studied under normal and drought conditions

Parameters	Number of tillers		Number of grains / spike		1000-grain weight		Grain yield / plant	
	Non-stress	Stress	Non-stress	Stress	Non-stress	Stress	Non-stress	Stress
D	2.99**± 0.31	14.4**± 0.39	23.7**± 4.49	193.80**± 14.1	6.080*± 2.58	26.1**± 4.89	0.51** ± 0.30	0.25 ** ± 0.41
H_1	1.48** ± 0.78	3.38**± 0.99	10.9 ** ± 11.4	72.68**± 35.83	12.95*± 6.56	25.3**± 12.40	8.64**± 0.75	5.12**± 1.01
H_2	0.92** ± 0.70	2.81**± 0.89	10.3** ± 10.2	73.49**± 32.03	10.8** ± 5.86	18.8** ± 11.1	5.47**± 0.67	4.34**± 0.91
F	-0.18** ± 0.7	0.09** ± 0.96	-1.2 ** ± 10.9	80.68**± 34.50	-6.77** ± 6.3	22.2** ± 11.9	1.11** ± 0.73	-0.1** ± 0.98
h^2	-0.27** ± 0.5	2.47**± 0.60	6.32 ** ± 6.87	165.9**± 21.5	-1.59** ± 3.9	9.63** ± 7.46	1.26**± 0.45	7.00**± 0.61
E	0.49**± 0.12	1.31**± 0.15	4.410**± 1.7	38.40**± 5.33	2.870*± 0.97	6.30**± 1.84	0.35**± 0.11	0.40**± 0.15
Proportion of components of variance								
$H_2/4H_1$	0.15	0.21	0.23	0.25	0.21	0.19	0.16	0.21
K_D/K_R	0.92	1.01	0.92	2.03	0.45	2.51	1.72	0.90
r (Yr.Wr+Vr)	0.83	0.33	0.91	-0.88	0.93	-0.78	-0.835	-0.60
$(H_1/D)^{1/2}$	0.70	0.48	0.68	0.61	1.46	0.98	4.11	4.52
$h^2_{(b.s)}$	0.81	0.86	0.78	0.66	0.78	0.61	0.88	0.80
$h^2_{(n.s)}$	0.72	0.79	0.65	0.49	0.57	0.32	0.43	0.27

D: additive variance, H_1 and H_2: dominance genetic variance and corrected dominance genetic variance, F: product of additive by dominance, h^2: square of difference P vs All, E: environmental variance, whole, $(H_1/D)^{1/2}$: average of degree dominance, $H_2/4H_1$: Proportion of genes with positive and negative effects in parents, K_D/K_R: Proportion of dominant and recessive genes in parents, r(Yr, Wr + Vr): correlation between parental measurement (Yr) and Wr+Vr values, $h^2_{(b.s)}$: heritability for diallel in a broad sense, $h^2_{(n.s)}$: heritability for diallel in a narrow sense. ns, * and **: non significant, significant at 5% and 1% of probability levels, respectively

Table 3: Estimates of genetic components of the mean for various traits studied in tree crosses under normal and drought conditions

Traits	Environments	[m]	[d]	[h]	[i]	[j]	[l]	χ^2
Salemer × Orizont								
Number of tillers	Non-stress	8.58**± 0.15	0.68**± 0.21	-	-	-	-	0.56
	Stress	6.3**± 0.139	2.12**± 0.20	-	-	-	-	0.37
Number of grains / spike	Non-stress	67.4**± 0.27	5.40**± 0.27	-20.56**±1.63	-	-5.09**± 1.9	18.29**± 1.81	1.69
	Stress	60.4**± 0.35	8.30**± 0.36	18.20**±1.94	-	-20.1**± 2.5	-8.49**± 2.06	4.01
1000-grain weight	Non-stress	29.37**± 3.3	3.43**± 0.54	41.53**±8.74	14.4**± 3.26	-9.88**± 2.7	-21.6**± 5.64	0.98
	Stress	35.9**± 0.55	6.92**± 0.55	19.25**±2.52	-	-8.51**± 2.8	-9.90**± 2.63	2.11
Grain yield / plant	Non-stress	10.1**± 0.14	0.87**± 0.13	4.57**±0.939	-	-	-2.38*± 1.070	3.82
	Stress	3.730**± 1.50	2.57**± 0.26	22.72**±3.99	3.72*± 1.48	-3.43**± 1.2	-17.1**± 2.58	0.63
Rihane × Pfyner								
Number of tillers	Non-stress	9.57**±0.14	0.53**±0.19	-	-	-	-	1.88
	Stress	6.50**±0.09	2.59**±0.13	-	-	-3.44**± 1.1	-	1.51
Number of grains / spike	Non-stress	63.6**±0.88	6.01**±0.28	6.71**± 1.25	7.45**± 0.94	-	-	2.73
	Stress	52.31**±0.2	12.2**±0.25	33.68**± 1.59	-	-18.3**± 2.16	-18.8**±1.74	0.31
1000-grain weight	Non-stress	42.29**±0.6	-2.99**±0.54	12.78**± 2.55	-	-	-7.99**±2.80	1.67
	Stress	5.470*±2.30	5.72**±0.39	87.60**± 6.18	27.5**± 2.28	-5.7**± 1.93	-56.7**±4.03	2.05
Grain yield / plant	Non-stress	10.3**±0.11	0.77**±0.16	-	-	-	-	1.33
	Stress	3.20**±0.97	2.59**±0.16	15.3**± 2.58	3.4**± 0.96	-1.83*± 0.8	-10.1**±1.71	0.80
Dana × Hemalaya								
Number of tillers	Non-stress	10.2**±0.123	0.74**±0.17	-	-	-4.47**±1.15	-	0.09
	Stress	7.47**±0.121	3.40**±0.27	-	-	-5.49**±1.12	-	3.84
Number of grains / spike	Non-stress	60.82**±0.32	6.20**±0.48	-	-	-	-	1.77
	Stress	32.55**±2.70	12.2**±3.93	79.19**± 7.15	15.76**± 2.6	-25.8**±2.19	-49.3**±4.65	0.02
1000-grain weight	Non-stress	46.25**±0.43	-1.9**±0.44	3.410**± 0.88	-	-	-	2.19
	Stress	22.98**±3.36	-	59.49**± 8.70	20.51**±3.34	-	-35.00**±5.58	2.82
Grain yield / plant	Non-stress	11.27**±0.07	1.04**±0.06	-12.22**± 0.34	-	-	12.43**±0.38	0.77
	Stress	6.690**±0.09	3.05**±0.09	-1.970**± 0.45	-	-	1.550**±0.48	3.31

[m]: Mean, [d]: Additive effects, [h]: Dominance effects, [i]: Additive × additive effects, [j]: Additive × dominance effects, [l]: Dominance × dominance effects, χ^2 :Chi-square

*, **: Significant at 5% and 1% level of probability, respectively

per plant in stress conditions, whereas F was positive and non-significant for grain yield under irrigated and 1000-grain weight under rainfed conditions. This parameter was positive and significant only for number of grains per spike in stress condition. However, dominant to recessive ratios (K_D/K_R) indicated that dominant genes were more frequent (ratio greater than 1) for number of grains per spike and 1000-grin weight in drought stress and grain yield in non-stress conditions (Table 2). Substantial effects of dominance due to heterozygous loci

(significant h^2) were significant for number of tillers and number of grains per spike under drought condition and grain yield per plant in both environments. Environment effect was significant for all the traits studied in both conditions.

To demonstrate more clearly the positive and negative effects of an accumulation of dominant and recessive alleles, the parental measurement (Yr) was correlated with parental order of dominance (Wr+Vr). This correlation was found negative for number of grains per spike and 1000-grain weight in stress and grain yield in both conditions, indicating that dominant genes contributed towards positive direction while number of grains per spike in normal and number of tillers in both environments were under the control of recessive genes (Table 2).

Generation Mean and Variance Analyses: There were significant differences among generations for different traits indicating the presence of sufficient genetic variability (data not shown).

Different 3 to 6 parameter models showed the best fits to generation means of different traits, conditions and cross combinations (Table 3).

In crosses Salemer × Orizont and Rihane × Pfyner, additive effects were significant for all traits in both environments. Also, in cross Dana × Hemalaya this parameter was significant for all traits except 1000-grain weight in drought condition. Non-significancy in this case may be ascribed to large error variance [35]. As is shown in Tables 3, some of the additive effects in crosses Rihane × Pfyner and Dana × Hemalaya were negative. The negative or positive signs for additive effects depend on which parent is chosen as P_1 [29, 36]. Dominance effects were positive and significant in cross Salemer × Orizont for all traits at both conditions, except number of tillers. Also, in this cross, negative and significant dominance effects were estimated for number of grains per spike in non-stress environment. In cross Rihane × Pfyner, these effects were significant for all traits in both conditions, except for grain yield per plant in normal and 1000-grain weight in both conditions. Also, in cross Dana × Hemalaya, except for number of grains per spike in normal and number of tillers in both conditions, dominance effects were significant for all traits studied. In this cross, these effects were negative for grain yield in both environments.

Table 4: Estimates of variance components for various traits studied in tree crosses under normal and drought conditions

Traits	Environments	D	H	F	Ew	$(H/D)^{1/2}$	Gs
Salemer × Orizont							
Number of tillers	Non-stress	7.54	2.36	0.11	1.11	0.56	39.9
	Stress	8.23	2.52	-0.49	0.87	0.55	57.6
Number of grains / spike	Non-stress	12.1	4.87	1.70	2.42	0.63	6.47
	Stress	4.53	25.1	-0.65	3.15	2.35	1.97
1000-grain weight	Non-stress	9.75	16.9	3.25	4.86	1.32	6.03
	Stress	8.16	18.8	0.87	6.57	3.01	4.99
Grain yield / plant	Non-stress	1.15	6.77	-0.23	0.79	2.42	5.85
	Stress	1.76	3.58	-0.68	1.08	1.42	9.94
Rihane × Pfyner							
Number of tillers	Non-stress	8.39	3.01	0.43	1.05	0.60	37.1
	Stress	4.35	2.85	0.82	0.35	0.81	37.5
Number of grains / spike	Non-stress	7.48	3.90	0.67	2.20	0.72	4.39
	Stress	2.83	23.0	-0.12	1.89	2.80	1.54
1000-grain weight	Non-stress	2.93	12.6	2.20	8.77	2.07	1.77
	Stress	3.03	8.88	1.92	2.87	1.71	3.45
Grain yield / plant	Non-stress	2.42	1.71	0.50	0.73	0.84	16.3
	Stress	0.79	0.76	0.10	0.62	0.98	8.95
Dana × Hemalaya							
Number of tillers	Non-stress	6.03	0.26	1.18	0.76	0.21	32.7
	Stress	2.80	0.29	0.38	1.05	0.32	24.5
Number of grains / spike	Non-stress	23.7	7.23	2.38	6.12	0.55	8.94
	Stress	4.68	14.1	-1.60	3.18	1.73	2.69
1000-grain weight	Non-stress	3.79	34.4	-0.15	5.58	3.01	2.05
	Stress	14.7	21.5	-0.96	4.82	1.21	8.14
Grain yield / plant	Non-stress	0.39	0.09	0.04	0.13	0.49	7.88
	Stress	0.27	0.53	0.08	0.22	1.41	6.88

D: Additive variance, H: Dominance variance, F: Correlation between D and H over all loci, E_W: Environmental variance,
$(H/D)^{1/2}$: Average degree of dominance, Gs: Genetic advance

Table 5: Estimates of the heritability by different methods for various traits studied in tree crosses under normal and drought conditions

Traits	Environments	Broad sense heritability ($h^2_{b.s}$)						Narrow sense heritability ($h^2_{n.s}$)
		Mahmud and Kramer (1951)	Warner (1952)	Allard (1960)	Allard (1960)	Mather and Jinks (1982)	Mean	
Salemer × Orizont								
Number of tillers	Non-stress	0.82	0.80	0.80	0.81	0.79	0.80	0.69
	Stress	0.84	0.84	0.84	0.83	0.84	0.84	0.73
Number of grains / spike	Non-stress	0.85	0.80	0.78	0.84	0.80	0.80	0.62
	Stress	0.78	0.75	0.77	0.77	0.76	0.76	0.19
1000-grain weight	Non-stress	0.59	0.64	0.63	0.59	0.62	0.62	0.35
	Stress	0.60	0.58	0.58	0.60	0.59	0.59	0.26
Grain yield / plant	Non-stress	0.88	0.82	0.79	0.88	0.82	0.82	0.19
	Stress	0.58	0.63	0.59	0.53	0.59	0.59	0.31
Rihane × Pfyner								
Number of tillers	Non-stress	0.87	0.85	0.83	0.85	0.82	0.85	0.70
	Stress	0.90	0.89	0.89	0.89	0.89	0.89	0.67
Number of grains / spike	Non-stress	0.73	0.70	0.70	0.73	0.68	0.71	0.54
	Stress	0.87	0.83	0.82	0.87	0.79	0.84	0.16
1000-grain weight	Non-stress	0.50	0.42	0.38	0.47	0.34	0.42	0.11
	Stress	0.53	0.55	0.55	0.53	0.56	0.54	0.23
Grain yield / plant	Non-stress	0.76	0.72	0.71	0.76	0.69	0.73	0.51
	Stress	0.57	0.52	0.51	0.57	0.49	0.53	0.33
Dana × Hemalaya								
Number of tillers	Non-stress	0.85	0.83	0.80	0.80	0.80	0.82	0.78
	Stress	0.40	0.58	0.51	0.37	0.58	0.49	0.55
Number of grains / spike	Non-stress	0.72	0.71	0.69	0.70	0.69	0.70	0.60
	Stress	0.66	0.65	0.65	0.66	0.65	0.65	0.26
1000-grain weight	Non-stress	0.73	0.69	0.73	0.67	0.65	0.69	0.12
	Stress	0.77	0.74	0.74	0.77	0.72	0.75	0.42
Grain yield / plant	Non-stress	0.74	0.68	0.66	0.74	0.63	0.69	0.56
	Stress	0.64	0.58	0.57	0.64	0.54	0.59	0.27

Average degree of dominance $[(H/D)^{1/2}]$ was less than unity for number of tillers in stress and non-stress environments and number of grains per spike in non-stress condition, in all crosses and for grain yield under irrigated condition in Rihane × Pfyner and Dana × Hemalaya crosses, suggesting the presence of partial dominance for these traits (Table 4). The fact that the estimated average degree of dominance was more than unity indicated the presence of over-dominance gene effects for rest of traits under different conditions and crosses.

Broad sense heritability estimates ranged from 0.59 (1000-grain weight and grain yield under drought stress) to 0.84 (number of tillers in stress condition) in cross Salemer × Orizont, from 0.42 (1000-grian weight under irrigated condition) to 0.89 (number of tillers under stress condition) in cross Rihane × Pfyner and from 0.49 (number of tillers in stress condition) to 0.82 (number of tillers in normal condition) in cross Dana × Hemalaya. Narrow-sense heritabilities ranged from 0.19 (grain yield under irrigated condition and number of grains per spike in

stress condition) to 0.73 (number of tillers in stress condition) in cross Salemer × Orizont, from 0.11 (1000-grain weight in normal condition) to 0.7 (number of tillers under irrigated condition) in cross Rihane × Pfyner and from 0.12 (1000-grain weight in normal condition) to 0.78 (number of tillers under irrigated condition) in cross Dana × Hemalaya. Also, Genetic advance ranged from 1.97 (number of grain per spike under stress condition) to 57.6 (number of tillers under rainfed condition) in cross Salemer × Orizont, from 1.54 (number of grain per spike under stress condition) to 37.5 (number of tillers in drought condition) in cross Rihane × Pfyner and from 2.05 (1000-grain weight in normal condition) to 32.7 (number of tillers under irrigated condition) in cross Dana × Hemalaya.

As it is shown in Tables 3, different types of epistasis interaction effects were found for different trait, cross and environment combinations. Additive × additive [i] non-allelic interaction was significant for 1000-grain weight and number of grains per spike under normal condition in crosses Salemer ×

Orizont and Rihane × Pfyner, respectively, number of grains per spike under rainfed condition in cross Dana × Hemalaya, grain yield under stress in Salemer × Orizont and Rihane × Pfyner crosses and 1000-grain weight under drought condition in Rihane × Pfyner and Dana × Hemalaya crosses. However additive × dominance gene action effect [j] was significant for all traits except grain yield under non-stress environment and number of tillers in both conditions in cross Salemer × Orizont and all of traits under irrigated condition in cross Rihane × Pfyner. This parameter was significant for number of grain per spike in rainfed condition and number of tillers in both of environment in cross Dana × Hemalaya. Non-allelic dominance × dominance [l] interaction was significant for all traits except number of tillers in both environments in cross Salemer × Orizont, number of grains per spike and grain yield in non-stress condition and number of tillers in both environment in cross Rihane × Pfyner. In cross Dana × Hemalaya this type of interaction was significant only for number of grains per spike and 1000-grain weight in stress and grain yield per plant in both conditions.

DISCUSSION

The results of present study confirmed that additive gene effects was revealed for number of tillers in both conditions by the significant D and [d] components from the diallel and generation mean analyses, respectively. Although epistatic variation (generally additive × dominance) exists for this trait, the narrow-sense heritability and genetic gain values indicated the predominance of additive gene action for expression of this trait. These results are in accordance with those by Mariey [37], Verma *et al.* [22] and Eshghi and Akhundova [23] who reported that additive and partial dominance genetic effects were important for number of tillers in different hulled and hulless barley populations. Thus, as shown here and in other studies for number of tillers selection should be effective in a conventional breeding program in the early generation in both drought and normal conditions.

In conclusion these results showed that epistasis was significant components of the genetic architecture of all traits, except number of grain per spike in normal and number of tillers in both conditions. Hence, detection, estimation and consideration of these components are important in formulating of breeding strategies. In cross Salemer × Orizont the signs of dominance [h] and dominance × dominance [l] gene effects were opposite for all traits at stress and non-stress conditions except

number of tillers suggesting duplicate type of non-allelic interaction in these traits. Also this kind of interaction was observed for number of grains per spike and grain yield in drought and 1000-grain weight in both environments in cross Rihane × Pfyner and number of grains per spike and 1000-grai weight under stress and grain yield in both conditions in cross Dana × Hemalaya. Since none of the signs of [h] were similar to the [l] type of epistasis, it was concluded that no complementary type of interaction was present in the genetic control of the studied traits.

Although in normal condition, generation means and diallel analyses showed that additive effects had a greater contribution than dominance effects for number of grains per spike, these analyses showed that dominance effects had a greater share in controlling this trait under drought condition. Reza *et al.* [38] reported that in barley, quantitative characters like number grains per spike in different cross combinations were affected by epistatic effectes and dominance type of gene action. In another research, Baghizadeh *et al.* [21] investigated the inheritance of yield and its components in P_1, P_2, F_1, F_2 and F_3 of a cross between Afzal and Cwb and reported that genetic control appeared dominance for this trait. Eshghi and Akhundova [23] found non-additive (non-fixable) type of inheritance for number of grains per spike in different barley populations too, but Verma *et al.* [22] reported additive (fixable) gene effects for this trait. Therefore, in non-stress condition where the additive gene action was present the selection in early generation may be fruitful however, in drought condition selection may be postponed to later segregating generations.

In all crosses, the dominance effects were greater than the additive effects for 1000-grain weight under both environments. Sharma and Sharma [39] performed diallel analysis for yield components including 1000-grain weight. The results showed that dominance gene action was important in the inheritance of 1000-grain weight. In another study, Baghizadeh *et al.* [21] showed that dominance and additive × additive [i] interaction as well as dominance × dominance [l] epistasis were important for inheritance of this trait and Wu and Takeda [40] opined that in general 1000-grain weight was governed by additive, dominance and non-allelic interactions. Also, Kularia and Sharma [41], Prakash *et al.* [42] and Nakhjavan *et al.* [43] reported different type of epistasis for this trait in barley under non-stress and drought conditions. The presence of interactions in the inheritance of 1000-grain weight in the present and earlier studies indicated that the trait is not simply inherited. The plants selected in early

segregating generation may not be expected to breed true. So, selection in later segregating generations may show good results. Some form of recurrent selection, such as bi-parental mating [44] or diallel selective mating [45] might prove to be an effective alternative approach.

Genetic gains as a parameter for selection efficiency are related to genetic variability, heritability and selection intensity. Low genetic gains and heritability obtained for grain yield compared to most of the other characters indicate that its phenotypic effect is mainly controlled by environmental variation. Therefore, for selection of the best genotype, we should concentrate mainly on yield components (such as number of grains per spike in normal condition and number of tillers in both conditions) than grain yield. Similar finding can be observed for grain yield per plant in works such as those accomplished by Ahmed [46], Ahmed *et al.* [47], Eshghi and Akhundova [23], Eshghi and Akhundova [48] and Nakhjavan *et al.* [43].

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