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Genetic analysis of grain yield and some agronomic traits in hulless barley

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The choice of an efficient breeding procedure depends to a large extent on the knowledge of the genetic system controlling the character to be selected. An eight-parent diallel, involving hulless barley varieties ICNBF-582, ICB-102607, ICNBF93-328, SB91925, ICNBF8-613, BBSC congana, Petuina2 and ICNBF93-369, was evaluated to determine the genetic parameters contributing to plant height, days to maturity, number of tillers, number of grains per spike and grain yield per plant. Furthermore, generation mean and variance analysis was carried out on six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) derived from the cross ICNBF93-369×ICNBF-582 and SB91925×ICB-102607 to complement the genetic information obtained from the diallel analysis. Wr/Vr graph in diallel analysis and average degree of dominance together with narrow-sense heritability values in both experiments revalued additive gene effects for plant height, number of tillers and days to maturity and over-dominance gene action for number of grains per spike. Although in cross ICNBF93-369×ICNBF-582 the dominance effects had a greater share, the additive effects in diallel analysis and cross SB91925×ICB-102607 played major role in the inheritance of grain yield per plant, since narrow-sense heritability of this trait was low. It can therefore be concluded that direct improvement of this trait is somehow problematic because environmental factors contribute greatly in the control of the trait.

Key words: Hulless barley, diallel, generation mean analysis, gene effects, agronomic traits.

INTRODUCTION

Barley (*Hordeum vulgare* L.) is one of the principal crops in the world and is classified into hulled and hulless barley according to the grain type. Hulless barley research and development is now receiving more emphasis with potential for feed, food and industrial uses. This crop is an important source of water-soluble plant fiber essential in human diets to lower serum cholesterol (Bhatty, 1986; Anderson and Berglung, 1990). Compared to hulled barley cultivars, hulless cultivars have lower fiber content and higher amount of starch due to absence of the hull. The crude protein of hulless barley typically exceeds that of comparable hulled types and should be 1-3% greater (Yang et al., 1997; Griffey, 1999). Hulless barley also has a major advantage over conventional barley in transportation, processing and storage. Removing the hull fraction, increases the bulk density (weight-per-unit volume) compared to conventional barley by about 25% (Newman, 1992; Bhatty, 1993). Hulless barley cultivars that are well-adapted to local conditions have been cultivated for a long time in many regions of the world. Thus, in southeastern and central Asia, its crops occupy 95% of the area, and in northeastern China, Korea, and Japan almost 50% of the area is under this crop (Anis'kov and Krolevets, 2008). Hulless barley is very well suited to Iran region fitting well with the cropping systems and potentially providing grain for the poultry industries in addition to current uses. Hulled barleys have not generally been fed due to their high fiber content while hulless barley has not been utilized because of the low yield varieties common in Iran region(Balouchi et al., 2005).

Grain yield is a complex trait made up of the interaction between different yield components and the environmental effects. Several studies in recent years have identified quantitative trait loci (QTLs) for yield and its components in barley. Cakir et al. (2003) reported three QTLs on chromosomes 2H, 3H and 5H for grain

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yield in barley. Li et al. (2006) reported several QTLs for yield and its components, such as number of grains per spike on chromosome 1H. Additionally, studies by Franckowiak and Lundqvist (2002), Buck-Sorlin (2002) and Babb and Muehlbauer (2003) have resulted in identification of major QTL low number of tillers (lnt) 1 on chromosome 3HL and a second QTL uniculm2 (cul2) on 6HL for a number of tillers. Also, Mohammadi et al. (2005) reported four QTLs on chromosomes 2, 5, 6 and 7 for days to maturity, and Chloupek et al. (2006) detected plant height QTLs on chromosomes 3H, 4H, 5H and 7H in barley.

The choice of an efficient breeding program depends to a large extent on the knowledge of gene action involved in the expression of the character. Different genetic cross designs such as generation mean, line×tester and diallel analyses were used to estimate gene action of yield and its components in barley. Among these methods, diallel analysis provides a unique opportunity to obtain a rapid and overall picture of genetic control of a set of parents in the early generation. On the other hand, in generation mean analysis, epistatic effects as well as additive and dominance effects can be estimated. Besides gene effects, breeders would also like to know how much of the variation in a crop is genetic and to what extent this variation is heritable. This is due to the fact that efficiency of selection mainly depends on additive genetic variance, influence of the environment and interaction between genotype and the environment.

The main objective of the present study is to identify genetic architecture of different important traits of hulless barley for further improvement of grain yield.

MATERIALS AND METHODS

Diallel analysis

The experimental material was composed of the following eight genotypes of hulless barley, all of which had been provided by ICARDA (International Centre for Agricultural Research in the Dry Area): (1) ICNBF-582 (6-rowed), (2) ICB-102607 (2-rowed), (3) ICNBF93-328 (6-rowed), (4) SB91925 (2-rowed), (5) ICNBF8-613 (6-rowed), (6) BBSC congana (6-rowed), (7) Petuina2 (2-rowed) and (8) ICNBF93-369 (2-rowed). These genotypes were crossed in a diallel fashion including direct crosses and their reciprocals during crop season 2006-2007. The 8 parents and their resulting 56 first filials (F_1s) were grown on November 2007, in a randomized block design with three replicates at Moghan region, Iran. Plots of parents and F_1s consisted of two rows of 2 m length with 30 cm spacing between rows and 10 cm between plants. Ten healthy vigorous plants in the parents and F_1s progenies were selected randomly for recording observations on 5 characters, namely: plant height (cm), days to maturity, number of tillers per plant, number of grains per spike, and grain yield per plant (g). 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 (1985). After that, data was subjected to graphical and component analyses according to Hayman (1954, 1957) and Jinks an Hayman (1953).

Analysis of parental measurements (Yr) and standard deviation graph of parental order of dominance (Wr+Vr) was accomplished following Johnson and Askel (1959).

Generation mean and variance analysis.

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 two combinations of the parental cultivars, ICNBF93-369 × ICNBF-582 and SB91925 × ICB-102607 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 (2007-2008) in a randomized block design with three replications at Moghan region. The row-length was always two meters but the number of rows varied as follows: three rows for the non-segregating P_1, P_2 and F_1 generations, 10 rows for F_2 generation, and 7 rows for the BC_1 and BC_2 generations since the non-segregating generations represent the homogeneous population while the segregating generations represent the heterogeneous population. The sample size (i.e. number of plants analyzed) varied as follows: 10 plants for the P_1, P_2 and F_1 generations, 70-75 plants for the F_2 generations, and 15 plants in the BC_1 and BC_2 generations.

Generation mean analysis was performed using the Mather and Jinks method (1982). In this method, mean of each character is expressed as follows:

Y= m + α [d] + β [h] + α² [i] + 2 αβ [j] + β²[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, [l] = sum of dominance×dominance interaction, and α, β, 2αβ and β² are the coefficients of genetic parameters. The genetic model that best fits the data was found by the mean of joint scaling test (Mather and Jinks, 1982), 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 (Kearsey and Pooni, 1996).

Broad-sense (h_b^2) and narrow-sense (h_n^2) heritabilities were estimated using the variance component method (Wright, 1968) and variance of F_2 and back cross generations (Warner, 1952), respectively, as:

$$h_b^2 = \{VF_2-[(VP_1+VP_2+2VF_1)/4]\}/VF_2$$

$$h_n^2 = [VF_2-(VBC_1+VBC_2)/2]/VF_2$$

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

$$R = i \times h_n^2 \times \sqrt{VF_2}$$

Variance components (additive, dominance and environmental) were estimated as described by Kearsey and Pooni (1996) and

Table 1. Mean of parents and F₁s for different traits in 8×8 diallel cross.

Genotypes	P.H	D.M	N.T	N.G.S	G.Y.P
1	87.73	194.5	4.50	61.4	9.34
2	83.85	194.6	4.61	63.1	7.76
3	80.09	189.8	5.97	58.8	9.88
4	80.79	200.5	6.45	65.3	10.77
5	73.47	197.8	5.41	61.9	9.14
6	84.42	203.2	4.62	59.7	7.49
7	87.41	204.8	5.45	58.9	9.05
8	83.72	203.2	6.11	64.2	10.21
1×2	91.68	196.8	5.02	60.1	10.03
1×3	85.31	191.4	4.37	59.5	10.47
1×4	93.08	193.6	6.12	57.3	10.23
1×5	85.63	191.4	5.85	58.6	9.73
1×6	93.14	201.0	4.47	58.9	10.72
1×7	92.10	192.0	5.41	59.6	9.14
1×8	90.30	193.0	5.27	60.2	8.73
2×1	89.13	192.0	5.32	59.1	8.91
2×3	85.76	190.9	5.56	59.6	9.19
2×4	92.32	192.0	5.85	61.4	9.71
2×5	84.99	198.4	5.20	58.4	8.70
2×6	90.03	201.6	5.00	57.8	8.63
2×7	92.00	196.8	5.51	60.5	9.14
2×8	86.78	190.4	5.42	58.7	9.05
3×1	85.50	192.0	6.55	59.5	10.91
3×2	87.67	190.9	5.67	60.9	9.44
3×4	81.87	193.0	6.24	59.9	10.33
3×5	82.13	191.4	5.98	61.4	9.88
3×6	82.38	193.0	5.71	54.6	9.50
3×7	90.00	192.0	6.12	55.4	10.17
3×8	90.85	194.1	6.24	54.1	10.49
4×1	88.12	196.2	6.25	57.2	10.27
4×2	91.68	195.7	5.67	59.4	9.36
4×3	85.57	191.4	6.12	61.2	10.27
4×5	85.69	195.7	6.55	63.0	10.86

Farshadfar (1998), using the following equations:

Additive variance: $V_{[d]} = (2VF_2 - VBC_1 - VBC_2)$
Dominance variance: $V_{[h]} = 4 (VF_2 - 1/2V_{[d]} - E)$
Environment variance: $V_E = 1/4 (VP_1 + VP_2 + 2VF_1)$
Average degree of dominance: $(H/D)^{1/2} = (V_{[h]}/V_{[d]})^{1/2}$

RESULTS AND DISCUSSION

Diallel analysis

The differences among the genotypes (parents and F₁'s of cross combinations) were highly significant for all the traits (data not shown). Significant differences among genotypes for grain yield and its related traits in different sets of material were also reported by Bhatnagar and Sharma (1995) and Rohman et al. (2006).

Both the scaling tests conducted [uniformity of Wr and Vr test (t^2) and regression coefficient test] revealed the absence of non-allelic interaction giving complete adequacy of the data for the additive-dominance model for all the traits. The mean values and genetic parameters for different traits estimated from diallel cross population are given in Tables 1 and 2, respectively.

The estimate of additive component (D) was significant for all the characters. Also the two measures of dominance viz. H1 and H_2 were highly significant for all the traits except for number of tillers and grain yield per plant. The average degree of dominance $[(H_1/D)^{1/2}]$ was less than unity for plant height, days to maturity, number of tillers and grain yield per plant, suggesting the presence of partial dominance for these traits (Table 2). Similar

Table 1. Contd.

Genotypes	P.H	D.M	N.T	N.G.S	G.Y.P
4×6	85.06	200.0	6.09	56.9	10.16
4×7	90.30	196.2	6.52	59.9	10.84
4×8	90.46	194.1	5.98	59.9	9.98
5×1	80.92	195.2	5.92	60.1	9.88
5×2	79.07	195.2	5.07	61.3	8.46
5×3	83.15	188.2	6.19	52.9	10.33
5×4	84.61	195.7	6.16	60.7	10.27
5×6	82.51	200.5	5.57	60.8	9.29
5×7	85.00	198.9	5.13	60.2	8.55
5×8	80.60	194.6	6.20	59.7	10.84
6×1	87.54	200.0	6.02	58.6	10.03
6×2	87.16	201.0	5.28	57.1	8.80
6×3	85.63	197.8	5.58	60.2	9.31
6×4	90.92	197.3	5.92	59.7	9.93
6×5	83.75	201.0	5.35	60.8	9.05
6×7	91.20	201.6	5.75	61.3	9.44
6×8	86.78	194.1	5.91	57.9	9.88
7×1	91.10	194.1	5.81	60.7	9.88
7×2	87.00	196.8	5.45	61.7	9.01
7×3	84.00	193.6	5.55	59.0	9.44
7×4	90.10	197.8	6.15	57.1	10.25
7×5	90.20	199.4	5.15	60.3	9.19
7×6	90.00	204.2	5.57	59.6	9.29
7×8	92.00	193.0	5.96	59.0	9.93
8×1	89.13	198.4	5.65	59.3	9.44
8×2	90.21	195.7	5.80	61.3	9.84
8×3	86.64	195.2	6.50	60.4	10.94
8×4	86.97	196.2	6.31	59.8	10.62
8×5	86.02	203.2	6.32	65.6	10.57
8×6	80.60	203.7	6.02	56.6	10.04
8×7	93.00	202.1	5.90	59.6	9.98
Mean	86.82	196.25	5.71	59.65	9.70
Mean parents	82.68	198.55	5.39	61.66	9.20
Mean F1	87.42	195.92	5.75	59.36	9.77
CV (%)	2.89	1.06	0.08	2.86	9.78
LSD$_{5\%}$	4.02	3.34	0.738	2.73	1.52

P.H = Plant height; D.M = days to maturity; N.T= number of tillers per plant;
N.G.S = number of grains per spike; G.Y.P = grain yield per plant.

finding can be observed for plant height, number of tillers, days to maturity and grain yield per plant in works such as those accomplished by Singh et al. (1999) and Budak (2000). Rohman et al. (2006) reported that both additive and non-additive components were important in controlling the inheritance of these traits, but dominance components were more predominant than additive. The fact that the estimated average degree of dominance was more than unity and the regression line intercepted Wr axis below the origin indicated the presence of over-dominance gene effects for number of grains per spike. Sharma et al. (2002), Rohman et al. (2006) and Ordas et

al. (2008) have also reported similar type of gene action for this trait in their studies.

Narrow-sense heritability of number of grains per spike (0.224) was low, while in plant height and grain yield per plant were medium enough (Table 2), and in days to maturity (0.712) and number of tillers (0.636) was almost high.

As the magnitude of H_1 is greater than H_2, the distribution of negative and positive alleles were therefore unequally distributed in the parents, and further proof of this unequal distribution of alleles over loci is provided by the ratio $H_2/4H_1$, which is less than its maximum value

Table 2. Components of diallel variance and their estimates for different traits in hulless barley.

Components	P.H	D.M	N.T	N.G.S	G.Y.P
$\hat{D}$	18.71**± 1.25	26.37**± 1.249	0.488**± 0.028	4.834**± 0.824	0.974**± 0.129
$\hat{H}_1$	0.643[n.s]± 2.95	8.51**± 2.95	0.1408**± 0.066	4.69*± 1.95	0.258[n.s]± 0.306
$\hat{H}_2$	18.362**± 2.87	16.39**± 2.87	0.117[n.s]± 0.064	9.73**± 1.89	0.31[n.s]± 0.298
$\hat{F}$	17.433**± 2.5	11.59**± 2.49	0.099[n.s]± 0.056	8.063**± 1.64	0.253[n.s]± 0.259
$\hat{h}^2$	67.46**± 1.68	20.52**± 1.67	0.371**± 0.037	15.72**± 1.1	0.85**± 0.174
$\hat{E}$	2.5**± 0.416	1.52**± 0.416	0.08**± 0.009	1.1**± 0.274	0.31**± 0.043
Proportion of components of variance					
$(H_1/D)^{1/2}$	0.99	0.788	0.49	1.419	0.56
$H_2/4H_1$	0.237	0.182	0.21	0.207	0.203
$[(4DH_1)^{1/2} + F / (4DH_1)^{1/2} - F]$	1.035	1.515	1.83	2.039	1.61
$R (W_r + V_r , Y_r)$	- 0.759	0.526	- 0.844	0.771	- 0.71
h_b^2	0.847	0.903	0.722	0.726	0.592
h_n^2	0.581	0.712	0.636	0.224	0.509

ns = non significant; * = significant at 5% of probability level; ** = significant at 1% of probability level; 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, $[(4DH_1)^{1/2} + F / (4DH_1)^{1/2} - F]$: Proportion of dominant and recessive genes in parents, $R (W_r + V_r , Y_r)$: correlation between parental measurement (Yr) and Wr+Vr values, h_b^2: heritability for diallel in a broad sense, h_n^2: heritability for diallel in a narrow sense

0.25 (Table 2). Positive F value for number of tillers, number of grains per spike and days to maturity suggested that dominant alleles were more abundant than the recessive ones in the parents, and this claim was supported by the ratio of $[(4DH_1)^{1/2} + F / (4DH_1)^{1/2} - F]$ which was more than unity.

The study of Wr/Vr and standard deviation graph in Figure 1 (a and b) showed that parent 7 had maximum number of dominant alleles, while parent 5 being away from origin carried maximum number of recessive alleles for plant height. Parental orders of dominance of standard deviation graph for days to maturity are in order of parents 3, 1, 6, 4, 2, 8, 5 and 7 (Figures 2a and b). For number of tillers, all the 8 parents were clustered in three groups viz. I (4), II (8, 3, 7, 2), and III (1, 6, 5). Parent 4 possessed the highest number of dominant alleles and parents 1, 6 and 5 had maximum recessive alleles for this trait (Figures 3a and b). For number of grains per spike, 1 and 6 possessed maximum dominant alleles while parents 8 and 4 had maximum recessive alleles being too far from origin (Figures 4a and b). In Figures 5a and b, it is obvious that parents 1 and 4 possessed maximum dominant alleles and parent 6 being away from origin carried maximum number of recessive alleles for grain yield per plant.

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 plant height, number of tillers and grain yield per plant, indicating that dominant genes contributed towards positive direction while number of grains per spike and days to maturity were under the control of recessive genes.

Generation mean and variance analysis

The result of variance analysis revealed significant differences for generation for all the characters investigated, being an evidence for presence of genetic variability and possibility of selection for yield and its components (data not shown).

Mean comparison (Table 3) between the genotypes showed that parents 1 and 3 outperformed parents 2 and 4 with respect to plant height, days to maturity, number of tillers and grain yield per plant, but performed almost similarly for number of grains per spike.

For the cross ICNBF93-369 × ICNBF-582, F_1 and F_2 mean performances were greater than the top parent for number of tillers. For this trait, BC_2 mean was close to superior parent whereas F_2 mean was lower than F_1. Also both F_1 and F_2 means for this cross were close to superior parents for plant height and number of grains
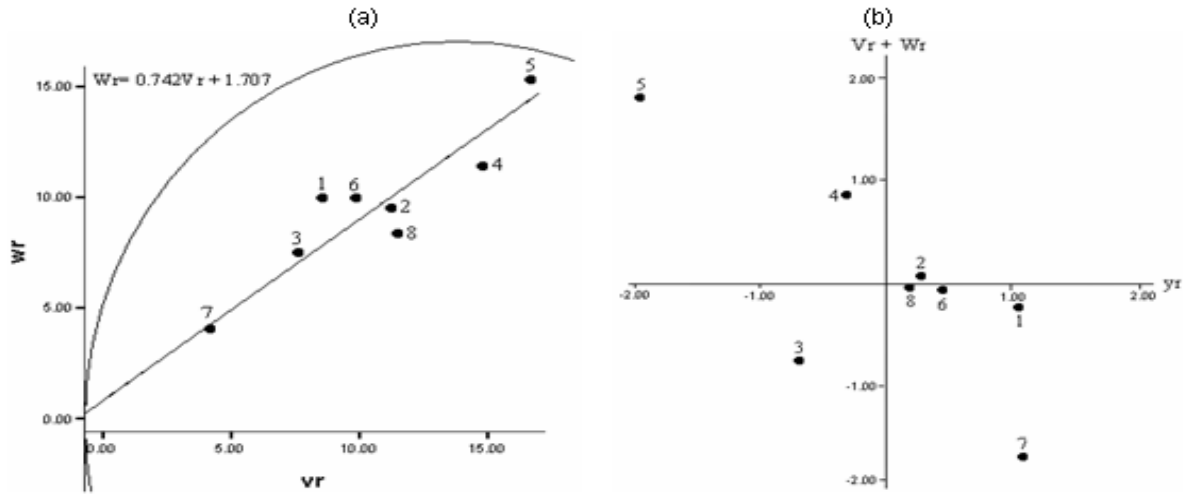
Figures 1. Wr-Vr and standard deviation graph of plant height.
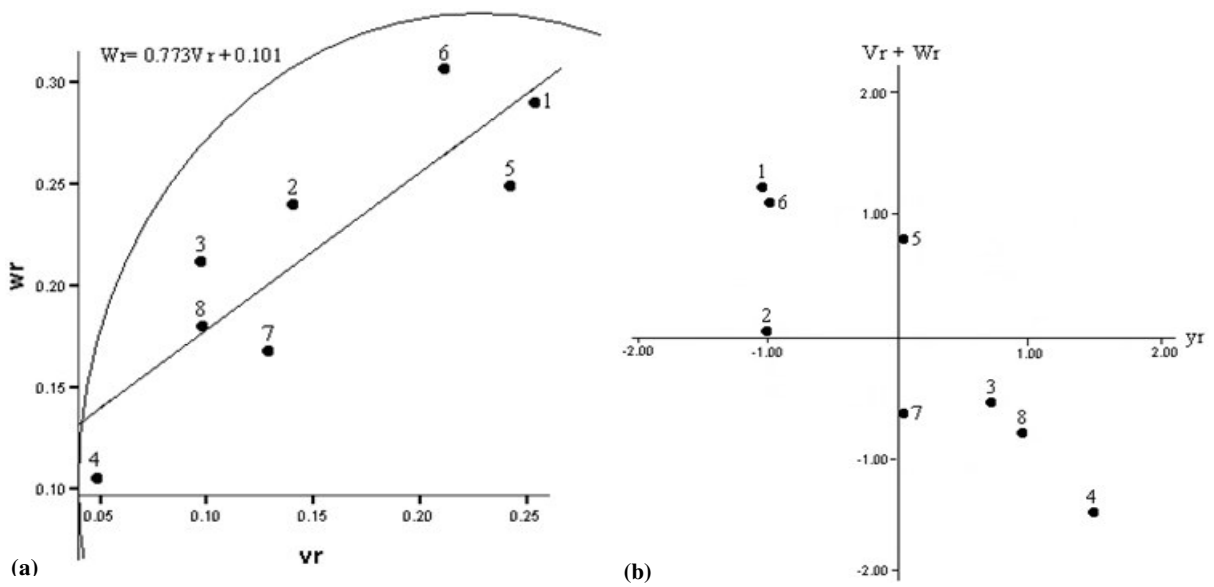
Figures 2. Wr-Vr and standard deviation graph of days to maturity.

per spike. Nevertheless, both BC generation means were greater than the top parents for these traits. In this cross, all the generation means except BC_2 for days to maturity were close to the earlier maturing parent. However, for grain yield per plant all the generation means were greater than or close to the top parent.

For the cross SB91925 × ICB-102607, F_1, F_2 and BC_1 means for plant height were lower than or close to the superior parent. Also in this cross for days to maturity, F_1 and BC_1 means were lower than or close to the earlier maturing parent, while F_2 and BC_2 means were between parental means. For number of tillers, F_1, F_2, BC_1 and BC_2 means were between parental means. However, all

the generation means exceeded the superior parent for number of grains per spike. Although F_1 mean for grain yield per plant in this cross was close to the top parent, F_2, BC_1 and BC_2 means were between parental means.

The estimates of genetic effects in six-parameter model are presented in Table 4. The estimated values of mean effects [m] were highly significant which indicated that all studied characters were quantitatively inherited. In both crosses, additive effects were significant for all traits. Nevertheless, estimates of genetic variance components showed that additive variance was greater than dominance for plant height, days to maturity and number of tillers in both crosses (Table 5). The average degree of
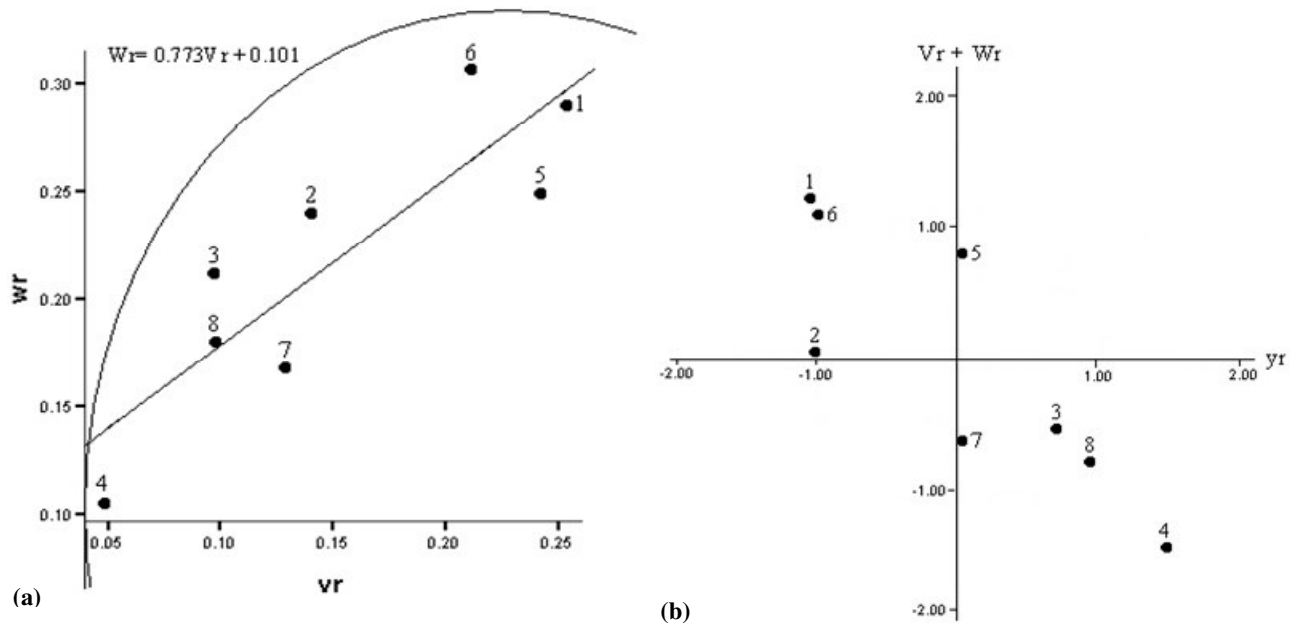
Figure 3. Wr-Vr and standard deviation graph of number of tillers.

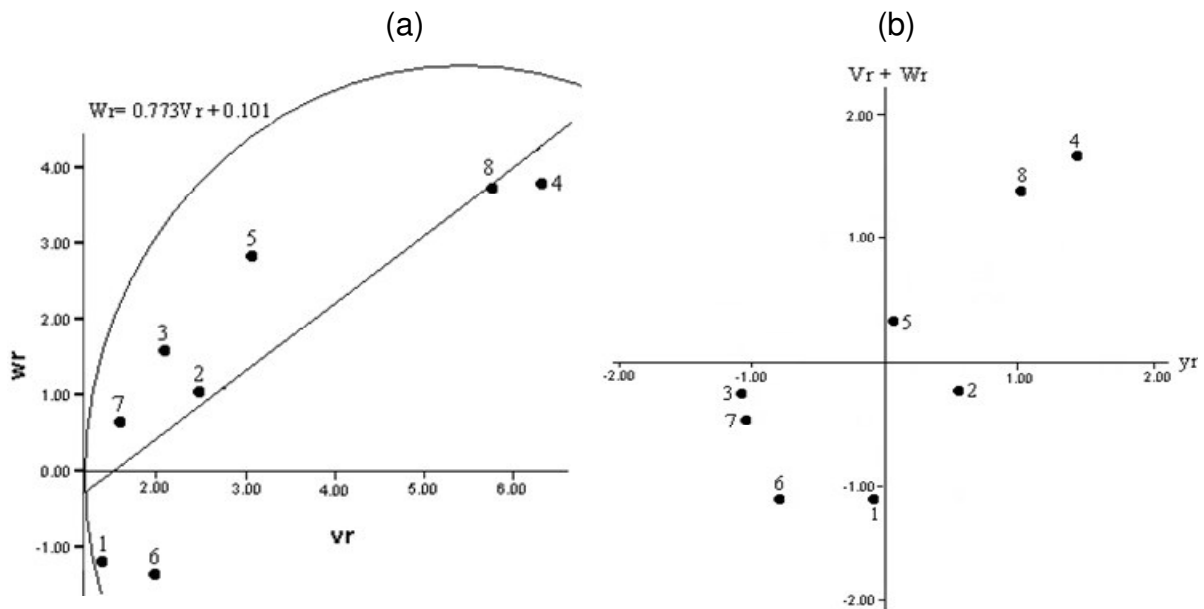**Figure 4.** Wr-Vr and standard deviation graph of number of grains per spike.

dominance was less than unity which indicated partial dominance gene action for these traits. Also for these traits, greater estimates of narrow-sense heritability and consequently greater gain from selection were found in both crosses (Table 5). These results are in accordance with those by Islam and Darrah (2005) and Verma et al. (2007) who reported that additive and partial dominance genetic effects were important for plant height, number of tillers and days to maturity in hulless and covered barley

genotypes, respectively.

Although in the cross ICNBF93-369 × ICNBF-582, dominance effects were positive and significant for plant height, number of grains per spike, and grain yield per plant, the greater ratio of $(H/D)^{1/2}$ from unity indicated over-dominance gene action only for number of grains per spike and grain yield per plant. Also in the cross SB91925 × ICB-102607, dominance effects were significant only for number of grains per spike. However,
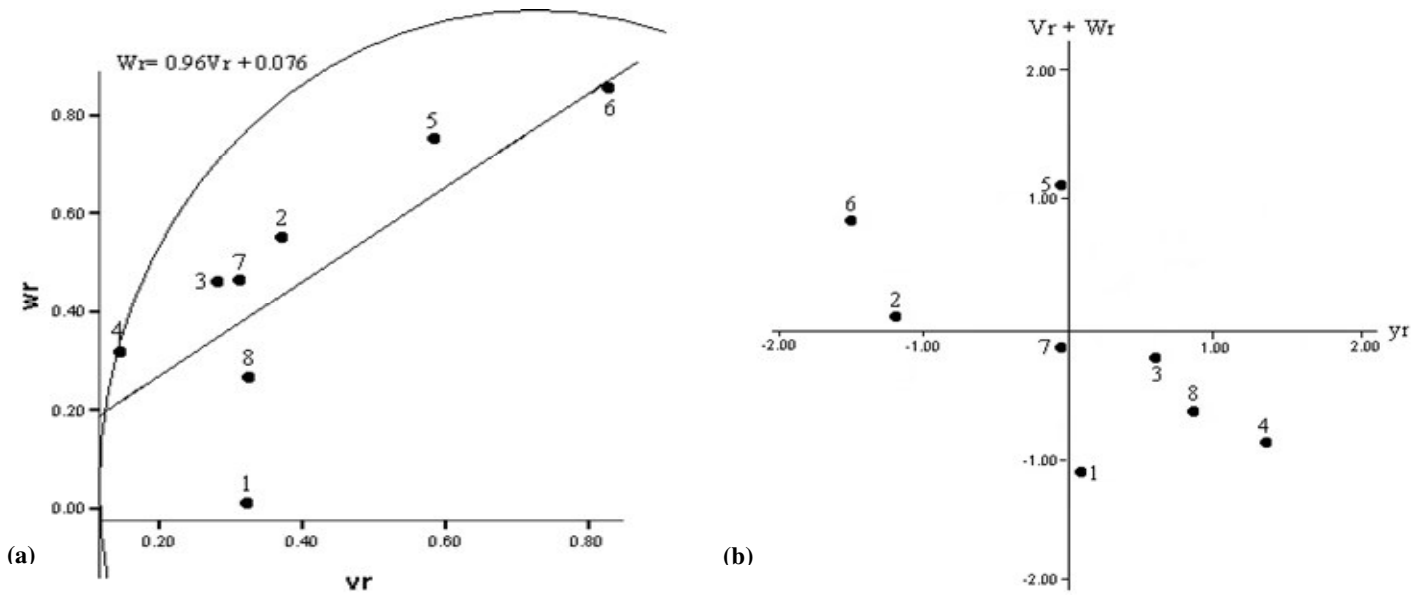
Figure 5 . Wr-Vr and standard deviation graph of grain yield per plant.

Table 3. Mean comparison between sub-main plots (genotypes) for various traits of the cross ICNBF93-369×ICNBF-582 and SB91925×ICB-102607.

| | Genotypes | | | | | |
Traits	P_1	P_2	F_1	F_2	BC_1	BC_2
ICNBF93-369×ICNBF-582						
Plant height	77.32e	86.82bc	83.2d	85.4cd	92.1a	89.2ab
Days to maturity	203.2a	196.2b	198.3b	196.2b	197.2b	203.4a
Number of tillers	6.41ab	4.51d	6.88a	6.58a	5.81c	6.31b
Number of grains / spike	60.37b	57.06c	58.82bc	59.04bc	65.19a	63.57a
Grain yield / plant	9.71c	8.27d	9.64c	11.3b	11.4ab	12.2a
SB91925×ICB-102607						
Plant height	79.52d	88.41b	85.2c	88.31b	91.24a	86.41bc
Days to maturity	203.1a	194.4de	195.4cd	197.2bc	192.9e	199.3b
Number of tillers	6.52a	5.02d	6.25b	6.2bc	6.01c	6.3b
Number of grains / spike	59.2d	55.12e	60.12cd	63.11ab	62.13bc	65.04b
Grain yield / plant	9.93a	7.67c	9.98a	8.87b	8.19c	8.96b

average degree of dominance showed that both additive and non-additive components of genetic variance were involved in governing the inheritance of this trait (Table 5). Although Baghizadeh et al. (2003) and Islam and Darrah (2005) found non-additive (non-fixable) type of inheritance for number of grains per spike and grain yield in covered and hulless barley accessions, respectively, Verma et al. (2007) reported additive (fixable) gene effects for these traits.

The epistatic types of gene interaction in each cross for different traits were found to be different from each other (Table 4). Additive×additive [i] non-allelic interaction was

significant only for number of grains per spike in the ICNBF93-369 × ICNBF-582 cross. However, additive × dominance gene action effect [j] was significant for plant height, days to maturity, number of tillers and grain yield per plant in the cross ICNBF93-369×ICNBF-582 and for all the traits in the cross SB91925×ICB-102607. Non-allelic dominance×dominance [l] interaction was significant for plant height and grain yield per plant in the ICNBF93-369 × ICNBF-582 cross and number of grain per spike in both crosses. The signs of dominance [h] and dominance×dominance [l] gene effects were oppo-site in the case of plant height and grain yield per plant in

Table 4. Estimates of genetic components of the mean for various traits studied in cross ICNBF93-369×ICNBF-582 and SB91925×ICB-102607.

Traits	M	[d]	[h]	[i]	[j]	[l]	χ^2
ICNBF93-369×ICNBF-582							
Plant height	63.11±15.12	-4.35±1.16*	73.2±36.31*	-	17.3±5.41*	-51.1±20.11*	3.6 (1)
Days to maturity	182.3±30.11	3.4±1.05**	-	-	-19.9±5.57*	-	6.74 (3)
Number of tillers	8.84±3.1**	0.97±0.21*	-	-	-2.7±1.01**	-	5.93 (3)
Number of grains / spike	38.15±7.46**	1.95±0.82*	68.3±17.2 **	21.36±7.72**	-	-40.91±9.9**	0.06 (1)
Grain yield / plant	6.79±1.2**	0.82±0.17*	14.44±3.16**	-	-3.44±0.74*	-11.8±1.73**	0.18 (1)
SB91925×ICB-102607							
Plant height	80.1±19.33**	-4.84±1.37*	-	-	19.35±7.62	-	6.3 (3)
Days to maturity	202.15±25.6	4.75±1.28	-	-	-21.1±6.33**	-	5.5 (3)
Number of tillers	5.65±2.11**	0.71±0.19*	-	-	-2.25±0.91*	-	2.7 (3)
Number of grains / spike	54.56±3.35**	2.44±0.33*	24.5±7.39**	-	-9.67±1.79**	-21.36±4.35*	0.6 (1)
Grain yield / plant	9.41±3.12**	1.19±0.33*	-	-	-3.77±1.32**	-	2.9 (3)

ns = non significant; * = significant at 5% level of probability; ** = significant at 1% level of probability; M = the mean of all generation; [d] = the sum of additive effects; [h] = the sum of dominance effects; [i] = the sum of additive × additive interaction; [j] = the sum of additive × dominance; [l] = the sum of dominance × dominance interaction**;** χ^2= Chi-square.

Table 5. Estimates of variance components and heritability for various traits in cross ICNBF93-369 × ICNBF-582 and SB91925×ICB-102607.

Traits	$V_{[d]}$	$V_{[h]}$	V_E	$(H/D)^{1/2}$	h^2_b	h^2_n	R
ICNBF93-369×ICNBF-582							
Plant height	28.51	6.19	2.257	0.46	0.87	0.79	7.97
Days to maturity	106.2	6.36	2.05	0.24	0.96	0.93	7.28
Number of tillers	1.41	0.092	0.102	0.25	0.87	0.85	24.16
Number of grains / spike	1.06	3.08	1.36	1.7	0.49	0.2	1.11
Grain yield / plant	0.032	0.078	0.04	1.56	0.47	0.21	1.04
SB91925×ICB-102607							
Plant height	32.0	7.7	4.37	0.49	0.80	0.72	7.86
Days to maturity	92.62	3.7	3.17	0.20	0.94	0.92	6.82
Number of tillers	0.3	0.12	0.07	0.63	0.72	0.6	9.89
Number of grains / spike	0.52	0.5	0.26	0.98	0.6	0.4	1.05
Grain yield / plant	0.39	0.29	0.262	0.86	0.51	0.37	6.25

$V_{[d]}$ = Additive variance; $V_{[h]}$ = dominance variance; V_E = environmental variance; $(H/D)^{1/2}$ = average degree of dominance; h^2_b = Broad sense heritability; h^2_n = Narrow sense heritability; R = genetic advance.

the cross ICNBF93-369 × ICNBF-582, and number of grains per spike in both crosses**,** suggesting duplicate type of non-allelic interaction in these traits. This kind of epistasis generally hinders improvement through selection and hence, a higher magnitude of dominance and dominance×dominance type of interaction effects would not be expected. It also indicated that selection should be delayed after several generations of selection (single-seed descent) until a high level of gene fixation is attained. Subsequent intermatings between promising lines may be important in accumulating favorable genes. Since none of the signs of [h] were similar to the [l] type of epi-

stasis, it was concluded that no complementary type of interaction was present in the genetic control of the studied traits. Although Islam and Darrah (2005) showed that non-allelic interaction effects were not important for plant height, number of tillers and days to maturity, Verma et al. (2007) reported additive×dominance and dominance × dominance type of epistasis for grain yield and its component in barley. Also Kularia and Sharma (2005) showed that duplicate type of interaction was prevalent in the cross RD2503×BL2 for days to maturity and in the cross RD2508×RD2502 for plant height, number of effective tillers and grain yield per plant. In another

study in hulless×covered cross barley using doubled haploid lines, Choo et al. (2001) reported additive × additive epistasis for yield and maturity.

Narrow-sense heritabilities ranged from 0.2 (number of grains per spike) to 0.93 (days to maturity) in the cross ICNBF93-369 × ICNBF-582, and from 0.37 (grain yield per plant) to 0.92 (days to maturity) in the cross SB91925 × ICB-102607 and genetic advanced ranged from 1.04 (grain yield per plant) to 24.16 (number of tillers) in the cross ICNBF93-369×ICNBF-582, and from 1.05 (number of grains per spike) to 9.89 (number of tillers) in the cross SB91925×ICB-102607.

The preponderance of additive gene effects was revealed for plant height, number of tillers and days to maturity by the significant D and [d] components from the diallel and generation mean analyses, respectively. Although epistatic variation (generally additive×dominance) exists for these traits, the narrow-sense heritability and genetic gain values indicated the predominance of additive gene action for expression of these traits. Thus, selection should be effective in a conventional breeding program in the early generation.

The results of the present study confirmed that the number of grains per spike is predominantly influenced by non-additive gene action. Due to presence of over-dominance type of gene action, selection of this trait will be difficult in the early generations. As selection based on progeny performance exploits only additive component of genetic variances, for this trait bi-parental mating followed by recurrent selection or diallel selective mating, which allows intermating among the selected segregates in the different cycles, would be useful to recover superior homozygote in later generations.

Although in the cross ICNBF93-369 × ICNBF-582 the dominance effects had a greater share, in diallel analysis and the cross SB91925×ICB-102607, the additive effects played the major role in the inheritance of grain yield per plant, since heritability of this trait was low. It can also be concluded that direct improvement of this trait is somehow problematic because environment has a great contribution in controlling this trait. Therefore, it is recommended that improving this trait in the population under study should be carried out through improving those traits which are correlated with it and are less controlled by environment and mostly controlled by genetic contribution.

In the population under study, additive effects formed the major part of variability for plant height and number of tillers. As a result, genetic improvement in the grain yield per plant would be easier through indirect selection for component traits such as plant height and number of tillers than through direct selection for grain yield.

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REFERENCES

Anderson JW, Berglung PT (1990). Oat-bran cereal lowers serum total and LDL cholesterol in hypercholesterolemic men. Am. J. Clin. Nuture 52: 495-499.

Anis'kov NI, Krolevets SS (2008). Study of naked barley cultivars of the VIR world collection under condition of the Siberian Irtysh River region. Russian Agric. Sci. 34: 293-295.

Babb S, Muehlbauer GJ (2003). Genetic and morphological characterization of the barley uniculm2 (cul2) mutant. Theor. Appl. Genet. 106: 846–857.

Balouchi HR, Tahmasbi Sarvestani Z, Modarres Sanavy AM (2005). Agronomic factors on selected hulless barley genotypes. J. Agric. 4: 333-339.

Baghizadeh A, Taleai A, Naghavi R, Khanaghah HZ (2003). Evaluation of some quantitative characters in barley using mean generation analysis. Iranian J. Agric. Sci. 35: 851-857.

Bhatnagar VK, Sharma SN (1995). Diallel analysis for combining ability for grain yield and its components in barley. Indian J. Genet. 55: 228-232.

Bhatty RS (1986). The potential of hull-less barley, a Rev. Cereal Chem. 63: 97-103.

Bhatty RS (1993). Physicochemical properties of roller-milled barley bran and flour. Cereal Chem. 70: 397-402.

Buck-Sorlin GH (2002). The search for QTL in barley (Hordeum vulgare L.) using a new mapping population. Cell Mol. Biol. Lett. 7: 523–535.

Budak N (2000). Heterosis, general and specific combining ability estimates at F_1 and F_2 generations of 8×8 diallel population in barley. Turk. J. Field Crops. 5: 61-70.

Cakir M, Poulsen D, Galwey NW, Ablett GA, Chalmers KJ, Platz GJ, Park RF, Lance RCM, Panozzo JF, Read BJ, Moody DB, Barr AR, Johnston P, Li CD, Boyd WJR, Grime CR, Appels R, Jones MGK, langridge P (2003). Mapping and QTL analysis of the barley population Tallon × Kaputar. Australian J. Agric. Res. 54: 1155-1162.

Chloupek O, Forster BP, Thomas WTB (2006). The effect of semi-dwarf genes on root system size in field-grown barley. Theor. Appl. Genet. 112: 779–78.

Choo TM, Ho KM, Martin RA (2001). Genetic analysis of a hulless covered cross of barley using doubled-haploid lines. Crop Sci. 41: 1021-1026.

Farshadfar E (1998). Application of biometrical genetics in plant breeding. Vol. 1, Razi Uni. Press. Kermanshah, Iran. p 537.

Franckowiak JD, Lundqvist U (2002). Current list of new and revised barley genetic stock descriptions. Barley Genet. Newslett. pp.32- 47.

Griffey C (1999). Hull-less barley as an improved feed crop. In: Small Grain Breeder. pp. 423-430.

Hayman BI (1954). The theory and analysis of diallel crosses. Genetics, 39: 789-809.

Hayman BI (1957). Interaction heterosis and diallel crosses. Genetics, 42: 336-355.

Islam AA, Darrah M (2005). Estimation of gene effects for seed yield and component traits in hulless barley. Turk. J. Field Crops. 8: 85-92.

Jinks JL, Hayman BI (1953). The analysis of diallel crosses. Maize Genet. Coop. Newsletter. 27: 48-54.

Johnson LPV, Askel R (1959). Inheritance of yielding capacity in a fifteen-parent diallel cross of barley. Can. J. Genet. Cytol. 1: 208-265.

Kearsey MJ, Pooni HS (1996). The genetical analysis of quantitative traits. Chapman and Hall, Inc., London. 381p.

Kularia RK, Sharma AK (2005). Generation mean analysis for yield and its component trait in barley (Hordeum vulgar L.). Indian J. Genet. 65:

129-130.

Li JZ, Huang XQ, Heinrichs F, Ganal MW, Roder MS (2006). Analysis of QTLs for yield components, agronomic traits, and disease resistance in an advanced backcross population of spring barley. Genome 49: 454-466.

Mather K, Jinks JL (1982). Biometrical genetics. Chapman and Hall, Inc., London. 396p.

Mohammadi M, Taleei A, Zeinali H, Naghavi MR, Ceccarelli S, Grando S, Baum M (2005). QTL analysis for phonologic traits in doubled haploid population of barley. Int. J. Agric. Biol. 7: 820-823.

Newman RK (1992). Nutritional quality. In: Sixth barley genetics symposium. Helsingborg, Sweden pp. 940-944.

Ordas M, Lamkey R, Rasul, N (2008). Diallel analysis of grain yield and its components in hulless barley. Turk. J. Field Crops. 8:110-119.

Rohman MM, Sultana R, Podder R, Tanjimul ATM, Islam MK, Islam MS (2006). Nature of gene action in barley (*Hordeum vulgar* L.). Asian. J. Plant. Sci. 5: 170-173.

Sharma Y, Sharma SN, Joshi P, Sain RS (2002). Combining ability analysis for yield and yield contributing characters in six-rowed barley. Sabrao J. Breed. Genet. 34: 55-63.

Singh I, Dashora SL, Sharma SN, Sastry EVD, Singh I (1999). Inheritance of some quantitative characters in six-rowed barley. Indian. J. Genet. 59: 99-101.

Singh RK, Chaudhary BD (1985). Biometrical methods in quantitative genetic analysis. Revised Ed. Kalyani pub. Ludhiana. New Delhi. 318p.

Verma AK, Vishwakarma SR, Singh PK (2007). Genetic architecture for yield and quality component traits over two environments in barley (*Hordeum vulgar* L.). Barley Genet. Newslett. 37: 24-28.

Warner JN (1952). A method for estimating heritability. Agron. J. 44: 427-430.

Wright S (1968). Evolution and the genetics of populations. Genetic and Biometric Foundation. The University of Chicago Press, Chicago 1: 371-420.

Yang WZ, Beauchemin KA, Ferr BI, Rode LM (1997). Comparison of barley, hulless barley and corn in the concentrate of dairy cows. J. Dairy Sci. 80: 2885-2895.