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Assessment of Gene Actions for Lodging Tolerance, Yield and Yield components of Barley (*Hordeum vulgare* L.)

Zerihun Jalata[1*], Firew Mekbib[2], Berhane Lakew[3] and Seid Ahmed[4]

[1]*Department of Plant Sciences, College of Agricultural Sciences, Wollega University, Ethiopia*
[2]*School Plant Sciences, College of Agriculture and Environmental Sciences, Haramaya University, Ethiopia, P.O.Box:138, Dire-Dawa.*
[3]*Ethiopian Institute of Agricultural Research (EIAR), Holetta Agricultural Research Center (HARC), P.O.Box: 2003 or P.O.Box 20420, Code 1000, Addis Ababa, Ethiopia.*
[4]*Biodiversity and Integrated Gene Management Program, ICARDA (International Center for Agricultural Research in the Dry Areas), Morocco.*

**Corresponding author*

Abstract

Information on genetic inheritance of quantitative traits is important to manipulate desirable genes. The aims of this study were to identifying superior parents and gene actions and interactions involved in controlling lodging and some agronomic characters on barley. Half 7x7 diallel analysis was conducted on 28 barley genotypes as well as generation mean analysis was done on six basic generations [F_1, F_2, BC_1, BC_2, P_1, P_2]in RCB design during 2014 and 2015 at Holetta, Ethiopia. The combining ability and generation mean analysis result showed the importance of additive (fixable) and non-additive (non-fixable) gene effects in the inheritance of all traits including lodging tolerance and grain yield. Grace and Sabini parents contained additive alleles for reducing plant height and lodging tolerance while HB42 and HB1307 had additive alleles for grain yield. Furthermore, generation mean analysis showed the prescience of non-allelic gene interaction for all characters studied. The three parameter model ([m], [d] and [h]) was adequate to explain the genetic variation for days to maturity, lodging severity at heading stage, physical test of straw strength and spike length. The finding suggests more additive effects of the genes have been expressed lodging tolerance in barley.

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Keywords

GCA and SCA gene effects, generation mean analysis, non-allelic gene interaction.

Introduction

Grain yield is one of the most important and complex traits in cereal breeding and depends upon a combination of different plant traits. Lodging and grain yield are negatively associated in barley (Mirosavljević *et al.*, 2015). The degree of lodging resistance in barley is significantly affected by the morphological traits of aboveground parts (stem length, strength, stem wall thickness, number and length of internodes, spike size and weight (Madić *et al.*, 2016). Barley crop suffers from considerable yield losses due to lodging in high yielding environments. Although the environmental factors such as the amount of available water and nutrient affect lodging, but prevention of lodging is possible to some degree using genetic resistance and most of the lodging

resistance genes are related to shorter plant stature (Kandemir, 2004). Therefore, grain yield increase in barley can be achieved by selecting plants with optimized plant height more resistant to lodging (Mirosavljević *et al.,* 2015).

Lodging in cereals refers to the displacement of culms from an upright position. Lodging is often associated with yield loss, with the magnitude of loss dependent on cultivar, growth stage, and the severity of lodging (Kelbert *et al.,* 2004). The level of yield losses depends on cultivar, growth stage, and lodging severity (Jedel and Helm, 1991). Depending on the growth stage and intensity of the problem, yield loss estimated due to lodging in barley varied by different authors. For instance, 20% (Briggs, 1990), 40% (Eassen *et al.,* 1993) and up to 66% (Berry *et al.,* 2003). Grain yields was reduced by 34% through induced lodging in barley at heading and by 24% twenty days after heading (Pinthus, 1973). Plant breeders have reduced lodging incident by introducing dwarfing genes to produce shorter varieties (Berry *et al.,* 2007). The exploitation of semi-dwarfing genes in barley breeding plays an important role in improving its productivity (Kuczyńska *et al.,* 2013).

The semidwarf reduced lodging and increased potential for high grain yield. Lodging resistant semidwarf barley cultivars have been successfully used in many parts of the world such as in China, and produced about five-fold yield increase over landraces and older cultivars (Zhang and Zhang, 2003.) and are widely applied in USA, Canada, most European countries, Japan and Korea as well (Hellewell *et al.,* 2000). Semidwarf genes normally results in 10-30 cm shorter plants and does not cause losses from potential yields and allow combine harvesting (Kandemir, 2004). The use of a dwarfing gene in breeding process is crucial for the development of modern cultivars. In barley, more than 30 types of dwarfs or semi-dwarfs, *sdw1/denso* locus, have been so far indicated. The semi-dwarfing cultivars had improved lodging resistance and a higher harvest index (Kuczyńska *et al.,* 2013).Therefore, the information on the gene effects and their interaction influencing the expression of the trait is useful to improve yield.

Diallel analysis is one of the most powerful tools for estimating the general combining ability (GCA) of parents and selecting of desirable parents and crosses with high specific combining ability (SCA) for the exploitation of heterosis (Sarkar *et al.,* 2002). Despite the fact that diallel is effective and widely used (Patil, 1997), it fails to detect epistasis or non-allelic interaction of genes (Sharma *et al.,* 2003). In comparison, generation mean analysis is useful technique in plant breeding for estimating gene effects (additive and dominance) and their dysgenic interactions (Kearsey and Pooni, 1996).The presence or absence of epistasis can be detected through the generation mean analysis using scale test that measures epistasis accurately whether it is additive x additive (complementary) or additive x dominance (duplicate) and (dominance x dominance) at disgenic level responsible for inheritance of quantitative traits (Sharmila *et al.,* 2007; Farshadfar *et al.,* 2008).

Thus, lodging resistance in barley can be improved based on selection of alleles affecting culm strength, wall thickness, plant height, and plant weight. Hence understanding about lodging will provide a theoretical basis for breeding programs designed to increase lodging resistance based on selecting desirable cultivars for attaining desired yield (Chen *et al.,* 2014).Resistance to lodging was also among the focus of hybridization programs in barley breeding in Ethiopia (Berhane *et al.,* 1996) however, there is very limited information available. Therefore, the extent of different gene actions involved controlling lodging tolerance and other agronomic characters was not identified which would be useful for improving lodging resistance via hybridization programs. In view of this, the present study was initiated with the aim of identifying superior parents and investigate the nature and magnitude of gene actions and interactions involved in controlling lodging and some agronomic characters on barley.

Materials and Methods

Experimental materials

Seven barley cultivars with diverse characteristics were crossed in 7x7 half diallel cross in 2014/15 main cropping season (June to December) at Holetta Agricultural Research Center, which is about 30 km west of Addis Ababa city, Ethiopia, to obtain 21 F_1 cross seeds. Barley parents include Sabini and Grace (short plant height, resistant to lodging, high yielding potential), Misrach (tall plant height, susceptible to lodging but high yielding potential), HB1307 (medium plant height, resistant to lodging and with high yielding potential), Miscal-21 (medium plant height, susceptible to lodging and with high yielding potential), HB42 and Agegnehu (six rowed, tall plant height, susceptible to lodging but high yielding potential). To supplement the diallel analysis, six basic generations such as F_1 and F_2 (first and second filial generations), and BC_1, BC_2 (first

and second back crosses) were developed from HB1307 (P_1) and Misrach (P_2) parents during 2014 and 2015 at Holetta, Ethiopia. The parents of the respective back crosses were used as male parent and the F_1 generation as female parent to obtain 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 was selfed to obtain F_2 seeds. F_1 hybrid seeds were obtained by hand emasculation and pollination in the field.

Planting methods

Seeds of each of 28 genotypes (7 parents + 21 F_1 hybrids) were sown in a plot size with two rows of 2.5 m length and 0.20 m width at 0.15 m spacing between plants in a randomized complete block design with three replications during 2015 main cropping season for field condition at Holetta Agricultural Research Center, Ethiopia. For evaluation of six basic generations, barley seeds were sown in variable rows as follows: two rows of P_1, P_2 and F_1 generation, six rows for F_2, and five rows in both BC_1 and BC_2 generations in RCB design in three replications during the same planting season.

Data collection

Data were recorded on days to heading, days to maturity, plant height, lodging severity (1-9 scale) score at heading and grain filling Zadok'sstages (Zadoks *et al.*, 1974) as modified by Tottman and Makepeace (1979), physical test of straw strength (1-5 scale, 1=very weak, 5=very strong) during grain filling stage, spike length, number of kernels per spike, thousand kernel weight and grain yield per plant on randomly tagged 10 plants per plot for diallel analysis while for generation mean analysis, the number of plants sampled/plot in HB1307 x Misrach cross varied as follows: five to ten plants for the P_1, P_2 and F_1 generations, 20-50 plants for the F_2 generation, and 15-20 plants in the BC_1 and BC_2 generations for plant height, lodging severity (1-9 scale) score at heading and grain filling growth stages, physical test of straw strength (1-5 scale) at 83 stage, spike length, number of kernels per spike, thousand kernel weight and grain yield per plant.

Statistical Analysis

Diallel Analysis

Analysis of variance (ANOVA) was performed using GLM procedures of SAS software (SAS, 2008). And then estimation of GCA and SCA were obtained following Griffing (Griffing, 1956) Method, model 1 (fixed) using Diallel SAS program (Zhang *et al.*, 2005).

Generation Mean Analysis

Scaling tests and generation mean analysis were done using SPAR2.0 (Statistical Package for Agricultural Research software version 2.0) (SPAR2.0, 2003). Thus generation mean analysis, means and variances were calculated as suggested by Hayman (1958).

In the presence of epistasis by scale tests, mean [m], additive [d], dominance [h] gene main effects and non-allelic interaction components were estimated to explain the inheritance of all the traits using Hayman (1958).

Individual scaling tests were applied according to Mather (1949) and Hayman and Mather (1955) to test the adequacy of the additive dominance model to explain the gene effects. Generation mean analysis was performed using Mather and Jinks (Mather and Jinks, 1982) method to detect the presence of non-allelic interactions of gene effects. Moreover, the joint scaling test (Cavalli, 1952)' was used to detect the epistasis for all characters measured. The three-parameter model (Jinks and Jones, 1958) was used to explain the genetic variation for those traits which showed non-significant values for χ^2 (Chi-square) tests. The adequacy of the model was tested by χ^2test. By observing a significant χ^2 value, the six parameter model was used to accommodate the digenicepistastic interactions.

Moreover in generation mean analysis, the genetic parameters were tested for significance using t-test. The best-fitted model was chosen as the one that had significant estimates of all parameters along with non-significant Chi-square.

Then the type of epistasis was determined by assuming the significance and sign of dominance [h] and dominance x dominance [l] effects.

When these effects were significant and had the same sign, the effects were complementary, while different signs indicated duplicate epistasis (Kearsey and Pooni, 1996). Variance components were estimated as described by Kearsey and Pooni (1996) using the following equations: Environment variance-V[E] = 1/4 (VP_1 + VP_2 + $2VF_1$), Additive variance - V[d] = ($2VF_2$ –VBC_1 – VBC_2), Dominance variance - V[h] = 4 (VF_2 –$1/2V_{[d]}$ – V[E]),Average degree of dominance- $(H/D)^{1/2}$= $(V[h]/V[d])^{1/}2$, F = (V_{BC1} -V_{BC2}), where V-stands for

variance and the subscripts refer to generations. F is the association between H and D at all loci.

Broad (h^2b) and narrow sense (h^2n) heritabilities were estimated using the formula proposed by Burton (1951) and Warner (1952) and the expected genetic advance from selection was calculated using the formulae proposed by Johnson *et al.,* (1955).

The mid parent heterosis (MPH) and better parent or heterobeltosis (BPH) were expressed as the percentage deviation of F_1 mean performance from the mid parent and better-parent values, respectively, as suggested by Wynne *et al.,* (1970). Inbreeding depression (ID) was also computed according to Singh *et al.,* (2004) and significance test was performed for ID, MPH and BPH by comparing the calculated 't' value with the table 't' value at 5% and 1% levels of significance.

Results and Discussion

Combining Ability Analysis

Analysis of variance combining ability showed that genotypes (7 parents + 21 F_1 hybrids) differed significantly (P<0.01) (Table 1) for general combining ability (GCA) for all characters studied except for physical test of stalk strength. Moreover, SCA also varied significantly (P<0.01) among genotypes for spike length, lodging severity scores per plot recorded at heading and grain filling stages, number of kernels per spike, and thousand kernel weight. The narrow sense heritability obtained from diallel analysis was from medium to high for the studied characters (Table 1). Large proportion of genotypes had shown greater mean performances over the parental means for different agronomic traits (Table.2).

GCA and SCA Gene effects

The estimates of GCA and SCA gene effects of parents and F_1 hybrids for lodging characters and other agro-morphological characters are presented in Table 2. Thus, Grace and Sabini parents showed highly significant negative GCA effects for plant height and lodging severity at heading stage.

And there was a highly significant and positive GCA effect for HB42 and HB1307 parents in grain yield per plant. Furthermore, comparison among the three parents, Sabini, Grace and Misrach, with highly negative significant GCA effects for plant height showed that Grace was significantly superior to the other two parents (Table 2). Estimates of SCA effects indicated that among 21 total crosses, 10 crosses (47.6%) had negative SCA effects for plant height which is in desirable direction. Specific crosses such as Sabini x Misratch, Grace xMisrach and Misrach x HB42 had highly significant SCA effects. Maximum highly significant positive SCA effect for grain yield was obtained in HB1307 x HB42 followed by Grace xMisrach. Thirteen crosses (61.9%) had shown positive SCA effects for grain yield per plant (Table 2).

Generation Mean Analysis

There were significant differences among generation means for all traits except for spike length, number of kernels per spike, thousand kernel weight and grain yield per plant (Table 3). The percentage of mid parent heterosis was negative for days to heading, days to maturity and lodging severity at heading and grain filling stages whereas the rest of studied traits showed positive heterosis. The estimates of inbreeding depression were positive for all traits measured except days to maturity, and lodging severity score at heading and grain filling stages (Table 3). The estimates of scaling tests and components of genetic variation for all characters studied are presented in Table 4. Hence, the individual scale tests (A, B, C and D) for days to heading, days to maturity, plant height, lodging severity score at heading and grain filling stages, physical test of stalk strength, number of kernels per spike, thousand kernel weight and grain yield per plant was significant. The mean (m) was highly significant for all traits except grain yield per plant and days to heading; and the additive x additive [i] and additive x dominance [j] digenic non-allelic gene interactions were significant for days to heading. The result showed that the three parameter model ([m], [d] and [h]) was adequate to explain the genetic variation for days to maturity, lodging severity scores per plot recorded at heading stage, physical test of straw strength and spike length **(**Table 4). Genetic parameters and components of variance for characters studied in HB1307 x Misrach barley cross is shown in Table 5. The adequacy of additive–dominance model for the characters studied indicated in Table 4 may also be further tested by the type of alleles and non-allelic associations in the genetic variances by using the three parameter model (E, D and H) (Table 5). The result from Table 5 indicated that the dominance variance (H) was greater than the corresponding additive variance (D) for most of the characters studied. And the average degree of

dominance $(H/D)^{½}$ values were closer or greater than unity for all traits except days to maturity and plant height. Narrow sense heritability was highest for plant height (0.618) followed by number of kernels per spike (0.417) while the narrow sense heritability values for most of the rest of the traits were relatively low. Genetic advance as percentage of F_2 mean (ΔG %) (Table 5) was higher for number of kernels per spike (6916.2) followed by thousand kernel weight (1540.5%). The existence of significant GCA and SCA effects (Table 1) for many of characters studied revealed the involvement of additive and non-additive gene effects. Grace and Sabini parents were best general combiners for plant height and lodging severity while HB42 and HB1307 for grain yield. This result coincides with diallel analysis of barley genotypes for the inheritance of stem height (Madić *et al.,* 2009) and lodging resistance and grain yield in barley (Singh *et al.,* 1996). The results showed most of the six rowed barley has shown high plant height and high lodging severity. Another finding showed that six rowed had higher lodging rate than two rowed line but short in height (Jezowski *et al.,* 2005). A lower lodging grade was accompanied by a decrease in plant height and an improved morphological and physical parameters (stemm diameter, wall thickness and stem elasticity (Rybinski *et al.,* 1998; Matušinsky *et al.,* 2015). The result revealed the high yielding potential HB42 and HB1307 parents would be better improved by hybridizing with Grace and Sabini parents and *vice versa* to incorporate lodging tolerance trait. Thus, Grace and Sabini parents can be suggested as useful parents as sources of genes for lodging resistance as they contain more additive alleles for plant height and lodging severity. This result is in agreement with Eshghi and Akhundova (2009) report on barley for grain yield per plant, plant height and days to maturity which was controlled by additive gene effect. Jezowski *et al.,* (2005) indicated the significance of the additive gene action determining resistance to lodging. In addition, this study is also partly agrees with the report of Raikwar (2015) on inheritance of thousand grain weight, and grain yield per plant were controlled by additive and nonadditive types (dominance and epistasis) of gene interaction. And other finding (Eshghi and Akhundova, 2010) on ICNBF93-369× ICNBF-582 barley cross indicated non-allelic dominance × dominance [l] interaction was significant for plant height and grain yield per plant. Hence, this may indicate the nature of alleles varies with the genotype, environment and its interaction. The F (direction of dominance) value was zero or positive for days to heading, days to maturity, lodging severity scores at heading stage, physical test of stalk strength, spike length, number of kernels per spike and grain yield indicating dominant genes in the high performance parent according to Said (2014). While F value was negative for plant height, lodging severity at grain filling stage and thousand kernel weight (Table 5) revealing dominant genes in the low performance parent of cross. The procedure indicated by Said (2014) showed that if the ratio of $F/\sqrt{DxH}$ is equal to or near one confirms indicates the magnitude and sign of dominance for all the genes monitoring the character is equal therefore the ratio $(H/D)^{½}$ is a good estimator of dominance while if the ratio of $F/\sqrt{DxH}$ is equal to zero or close to zero, the magnitude and sign of the genes controlling the character is not equal and hence $\sqrt{H/D}$ explains average dominance(Said, 2014). Hence, the average degree of dominance $(H/D)^{½}$ values sowed over dominance for all traits except days to maturity and plant height while plant height showed partial dominance.

Therefore, selection of characters controlled by dominant genes should be delayed until late generation. And, the F estimate and average degree of dominance values showed that dominance was unidirectional negative decreasing alleles at all loci for plant height, lodging severity at grain filling stage, thousand kernel weight while unidirectional positive increasing alleles for days to heading, lodging severity scores at heading stage, physical test of stalk strength, spike length, number of kernels per spike and grain yield. In addition to this, narrow sense heritability and genetic advance as percentage of F_2 mean (ΔG %) (Table 5) was higher for number of kernels per spike, thousand kernel weight, lodging severity score at grain filling stage and plant height indicating phenotypic selection based on these traits would be effective to improve these traits

According to Ebadi-Segherloo *et al.,* (2016) heritability coupled with high genetic advance (GA) would be more useful tool in predicting the resultant effect in selection of the best genotypes for yield and its attributing traits as well as helps in determining the influence environment on the expression the genotypic and reliability of characters. This study is in agreement with Singh (2014) report on narrow-sense heritability indicating predominance of additive gene action for expression of plant height, number of tillers and days to maturity in barley *via* diallel and generation mean analysis. Similarly, highest value of narrow sense heritability was recorded in another study for hundred grain weight (Ebadi-Segherloo *et al.,* 2016).

Table.1 Analysis of variance for lodging and other agro-morphological characters ofbarley in 7x7 half diallel

Source of variation	DF	DH	DM	PH	Lodg1	Lodg2	PhT	SPL	Nk/Spk	TKW	GY/Pl
Replication	2	7.05	0.87	60. 5	12.0	13.6	0. 9	0.89	40.57	122.11	178.7
Genotypes	27	60.45**	43.02**	431.7**	11.7**	16.8**	0.5*	3.14**	548.99**	282.01**	237.0**
error	54	5.57	6.99	19.3	1.6	1.5	0.3	0.22	16.91	13.44	101.0
CV (%)	-	3.06	2.11	13.0	52.9	39.7	29.2	5.62	11.41	7.17	32.5
GCA	6	227.603**	155.85**	716.1**	31.2**	49.6**	0.4ns	7.192**	1683.501**	255.97**	467.4**
SCA	21	12.687ns	10.79ns	350.5**	6.2**	7. 5 **	0.5*	1.981**	224.844 **	289.45**	171.2 ns
Beker ratio	-	0.97	0.97	2.0	5.1	6.7	0.8	0.88	0.94	0.64	2.7
M'e	54	1.86	2.33	6.4	0.5	0.5	0.1	0.07	5.63	4.48	33.7
h^2n	-	0.940	0.922	0.667	0.824	0.862	0.414	0.778	0.880	0.465	0.695

*, ** significance at 0.05 and 0.01 probability levels, respectively, ns=non significance, CV (%)- coefficient of variation, DF-degree of freedom, M'e-mean square of error divided by number of replications, h^2n- narrow sense heritability, DH-days to heading, DM-days to maturity, PH-plant height, SPL-spike length, Lodg1 and lodg2 –lodging severity scores per plot recorded at heading and grain filling growth stages, respectively,PhT- physical test of straw strength, Nk/Spk-number of kernels per spike, TKW-thousand kernel weight, GY/Pl-grain yield per plant.

Table.2 Mean values, GCA and SCA gene effects of parents and F_1 hybrids for lodging and other agro-morphological characters in barley tested.

No.	Parent	PH		Lodg1		Lodg2		PhT		GY/Pl	
		Mean	GCA	Mean	GCA	Mean		Mean	GCA	Mean	GCA
1	Sabini	78.6^{m}	-3.0**	1.0^{e}	-1.0**	1.0^{f}	0.1	1.5^{abc}	0.1	17.9^{ghi}	-14.8**
2	Grace	65.1^{n}	-7.8**	1.0^{e}	-0.8**	1.0^{f}	-0.1	0.9^{f}	-0.1	13.0^{hi}	-7.3**
3	Misrach	90.0^{l}	-2.2**	8.3^{a}	2.1**	9.0^{a}	-0.1	1.1^{f}	-0.1	31.1^{bcde}	-1.2
4	HB1307	105.2^{defg}	4.5**	1.0^{e}	0.1	1.3^{f}	0.1	1.9^{abcd}	0.1	41.9^{abc}	14.6**
5	Miscal-21	90.4^{kl}	-0.5	1.7^{e}	-0.4*	1.7^{f}	-0.2*	1.1^{ef}	-0.2*	24.1^{ef}	-3.4
6	HB 42	107.7^{cdef}	7.9**	1.0^{e}	-0.6**	1.3^{f}	0.0	1.1^{bcdef}	0.0	25.0^{efgh}	10.4**
7	Agegnehu	93.9^{ijk}	1.1	2.7^{e}	0.6**	4.7^{e}	0.2*	2.0^{a}	0.2*	31.7^{cde}	1.6
	$SE_{(gi)}$		0.8		0.2		0.09		0.09		1.8
	$SE_{(gi-gj)}$		1.2		0.34		0.14		0.14		2.7
	Cross		**SCA**		**SCA**		**SCA**		**SCA**		**SCA**
1	Sabini x Grace	78.3^{m}	-12.7**	1.0^{e}	0.5	2.7^{cd}	2.2**	1.2^{cdef}	-0.5	19.4^{hi}	-15.1*
2	Sabini x Misrach	108.7^{cdef}	12.0**	1.7^{e}	-1.8**	2.0^{f}	-2.2**	2.0^{bcde}	0.3	28.2^{efg}	6.1
3	Sabini x HB1307	110.9^{bcde}	7.6**	1.7^{e}	0.2	2.0^{f}	0.1	2.1^{bcde}	0.2	24.9^{i}	0.8
4	Sabini x Miscal-21	105.5^{cdef}	7.2**	1.0^{e}	0.1	1.3^{f}	0.4	1.6^{def}	-0.1	27.8^{efgh}	2.7
5	Sabini x HB42	114.4^{a}	7.7**	1.3^{e}	0.5	1.7^{f}	0.1	2.5^{ab}	0.7*	24.8^{efgh}	12.3*
6	Sabini x Agegnehu	112.7^{abc}	-4.5	1.3^{e}	-0.1	1.3^{f}	-1.0	2.1^{bcdef}	-0.3	30.7^{efgh}	3.1
7	Grace x Misrach	103.9^{ghij}	12.2**	1.0^{e}	-2.6**	1.0^{f}	-3.2**	2.1^{abc}	0.5	40.6^{efg}	23.9**
8	Grace x HB1307	110.0^{abcd}	11.5**	1.0^{e}	-0.6	1.0^{f}	-0.9	2.3^{ab}	0.5	39.9^{bcde}	6.4
9	Grace x Miscal-21	103.1^{efghi}	9.7**	1.0^{e}	-0.1	1.0^{f}	0.0	1.8^{bcde}	0.3	34.5^{def}	9.7
10	Grace x HB42	111.2^{defgh}	9.4**	1.0^{e}	0.0	1.0^{f}	-0.6	2.0^{cdef}	0.3	29.7^{efgh}	10.2*
11	Grace x Agegnehu	107.1^{abcd}	-9.0**	4.3^{ab}	2.5**	4.3^{bc}	2.0**	2.1^{def}	-0.4	36.7^{efgh}	-7.0
12	Misrach x HB1307	98.9^{jkl}	-5.2*	7.3^{a}	2.8**	7.7^{ab}	2.1**	1.4^{ef}	-0.3	27.8^{fghi}	-23.9**
13	Misrach x Miscal-21	96.1^{hijk}	-3.0	5.0^{cd}	1.0	6.3^{cd}	1.6**	1.6^{cdef}	0.1	24.4^{efgh}	-11.1*
14	Misrach x HB42	108.4^{defg}	0.9	2.3^{de}	-1.6**	5.7^{de}	0.4	1.9^{bcde}	0.3	35.0^{bcde}	7.3
15	Misrach x Agegnehu	98.7^{ijk}	-9.4**	3.7^{de}	0.4	5.7^{cd}	0.2	1.8^{bcde}	-0.5	30.3^{efg}	-5.1
16	HB1307 x Miscal-21	108.1^{cdef}	2.3	1.0^{e}	-1.0	1.3^{f}	-1.0	1.6^{bcde}	-0.1	39.6^{a}	8.8
17	HB1307 x HB42	113.1^{ab}	-1.1	2.0^{cd}	0.1	4.3^{de}	1.4*	1.7^{bcdef}	-0.1	58.5^{a}	34.3**
18	HB1307 x Agegnehu	103.4^{fghi}	-9.6**	5.0^{bc}	0.3	6.3^{cd}	0.2	1.9^{bcde}	-0.1	38.6^{ab}	-17.3**
19	Miscal-21 x HB42	112.2^{ab}	3.0	2.0^{e}	0.6	2.0^{f}	-0.1	2.0^{ab}	0.4	25.6^{ef}	14.4*
20	Miscal-21 x Agegnehu	103.7^{defgh}	-8.9**	1.7^{e}	-0.7	2.0^{f}	-1.1	1.9^{abcd}	-0.3	30.6^{ef}	-9.5
21	HB42 x Agegnehu	110.6^{cdef}	-10.0**	3.3^{e}	0.6	5.3^{de}	0.1	1.9^{ab}	-0.8*	32.2^{abcd}	-39.3**
	$SE(Sij)$		2.3		0.7		0.6		0.3		5.2
	$SE(Sij-Sik)$		3.4		1.0		0.9		0.4		7.7
	$SE(Sij-Skl)$		3.2		0.9		0.9		0.4		7.2
	LSD (%)	7.20		2.05		1.99		0.84		16.45	
	CV(0.05)	4.32		52.85		39.66		29.17		32.54	

*, ** significant at 0.05 and 0.01 probability levels, respectively, $SE_{(gi)}$-standard error of all GCA, $S.E_{(gi-gi)}$- standard error of GCA for two GCA effects, $SE_{(Sij)}$-standard error for testing all SCA, $SE_{(Sij-ik)}$-standard error for comparing the difference between two SCA having one common parent, $SE_{(Sij-kl)}$- standard error for testing the SCA of two crosses having no parent in common. PH-plant height,Lodg1 and lodg2 –lodging severity scores recorded at 53 and 83 Zadok's scale, respectively, PhT- physical test of straw strength.

Table.3 Analysis of variance, generation mean and standard errors for various characters measured in HB1307 x Misrach barley cross.

Generation	df	DH	DM	PH	Lodg1	Lodg2	PhT	SPL	Nk/Spk	TKW	GY/Pl
Replication	2	4.2	2.4	6.1	3.4	2.7	0.1	0.5	0.2	6.5	6.5
Generation	5	30.4**	14.5**	28.5*	4.5*	12.6**	0.7**	0.5^{ns}	15.9^{ns}	15.1^{ns}	15.1^{ns}
Error	10	2.2	0.5	5.0	1.1	1.7	0.1	0.3	10.0	17.3	17.3
CV (%)		2.0	0.6	2.2	37.7	33.8	12.5	7.3	6.7	19.0	19.0
P1	-	80.7± 1.9	129.3± 0.7	95.0±2.1	1.0± 0.0	1.0 ±0.0	2.8±0.1	6.3±0.5	46.0 ± 1.5	44.3±1.0	24.33 ±2.06
P2	-	73.0± 0.6	122.7 ±0.3	99.3±0.9	2.7 ±0.3	5.3 ±0.3	1.5 ±0.0	7.0±0.4	49.7 ±2.7	35.7±2.3	20.87±4.50
F1	-	74.0±0.6	124.7±0.3	104.0±1.2	1.7 ±0.3	1.7 ±0.3	2.5 ±0.2	7.5±0.1	50.7 ±0.7	43.7±0.5	24.27±0.99
F2	-	72.0±0.0	125.0±0.6	101.7±0.3	3.3 ±0.7	4.7± 1.3	2.3 ±0.2	6.7±0.3	45.0 ±2.0	41.2±1.0	18.37±1.52
BC1	-	73.7±0.7	126.0±0.6	100.7 ±1.2	3.3 ±1.3	4.7 ±0.8	2.2 ±0.2	6.6±0.3	45.7 ±1.5	41.7±1.0	21.53 ±1.79
BC2	-	72.7±0.7	125.0±0.6	102.0±1.5	4.3±0.7	6.0 ±1.0	1.7 ±0.1	7.0±0.2	47.3 ±0.9	41.3±1.9	21.93 ±0.20
MP heterosis (%)	-	-3.7	-1.1	7	-9	-47	15.7	12.4	5.9*	9.3	7.4**
BP heterosis (%)	-	1.4	1.6	9.5	67	67	-10.8	7.2	2**	-1.3*	-0.2**
ID (%)	-	2.7	-0.3	2.2	-99	-179.6	13.8	10.7	11.2**	5.7*	24.3**

Note: *, ** significance at 0.05 and 0.01 probability levels, respectively, ns=non significance, CV (%)- coefficient of variation, df-degrees of freedom, DH-days to heading, DM-days to maturity, PH-plant height, SPL-spike length, Lodg1 and lodg2 –lodging severity scores per plot recorded at heading and grain filling growth stages, respectively, PhT- physical test of straw strength, Nk/Spk-number of kernels per spike, TKW-thousand kernel weight, GY/Pl-grain yield per plant, ID (%) = inbreeding depression, MP=mid parent, BP=better parent

Table.4 Estimates of scaling tests, and types of gene action using generation means for various studied characters in HB1307 x Misrach Barley cross.

Parameters	DH	DM	PH	Lodg1	Lodg2	PhT	SPL	NK/Spk	TKW	GY/Pl
Scaling test										
A	-7.3±2.4*	-2.0±1.4	2.3±3.4	4.0±2.7	6.7±1.8**	-0.9±0.5	-0.7±0.8	-5.3±3.4	-4.5±2.2*	-5.5 ±4.2
B	-1.7±1.6	2.7±1.3*	0.7±3.4	4.3±1.4**	5.0±2.1*	-0.6±0.3*	-0.5 ±0.5	-5.7±3.3	3.2±4.5	-1.3 ±4.6
C	-13.7±2.3**	-1.3±2.5	4.3±3.5	6.3±2.8*	9.0 ±5.4	-0.7±1.0	-1.6 ±1.2	-17.0±8.7*	-2.7±4.8	-20.3 ±8.1*
D	-9.7±1.9**	-2.0±2.7	9.0±2.7**	3.0±3.0	3.0 ±6.0	-0.0 ±1.1	0.03 ±1.3	-5.7±9.5	2.4±5.2	-8.5 ±8.4
Three parameter model										
m	72.2±2.1**	124±2.9**	98.5±4.2**	-0.2±4.0	0.5±6.0	2.9±1.1**	6.2±1.3**	41.8±8.8**	38.6±6.0**	9.1±7.5
[d]	3.8±1.0**	3.3±0.4**	-2.2±1.1	-0.8±0.2**	-2.2±0.2**	0.6±0.1**	0.3±0.3	-1.8±1.5	4.3±1.3**	1.7±2.5
[h]	-2.5±6.4	3.33±6.8	7.2±12.5	12.1±10.4	15.5±13.3	-2.7±2.5	0.5±3.1	3.8±19.5	5.1±15.7	21.8±17.9
Gene effects, six parameter model										
m	72.0±0.0	125.0± 0.6**	101.7± 0.3**	3.3** ± 0.7	4.7** ±1.3	2.1** ±0.2	6.7 ±0.3**	45.0** ±2.0	41.2** ±1.0	18.4 ±1.5
[d]	1.0±0.9	1.0±0.8	-1.3± 1.9	-1.0 ± 1.5	-1.3±1.3	0.5±0.3	-0.4 ±0.4	-1.7±1.7	0.4±2.2	-0.4±1.8
[h]	1.8±2.2	0.7± 2.9	5.5± 4.4	1.8 ±4.0	1.2 ±6.0	-0.3 ±1.1	1.2 ±1.3	8.8±8.9	5.1±6.1	15.1±7.6
[i]	4.7±1.9*	2.0± 2.8	-1.3± 4.1	2.0 ±4.0	2.7 ±6.0	-0.8±1.1	0.4 ±1.3	6.0 ±8.7	1.3±5.9	13.5±7.1
[j]	-2.8 ±1.4*	-2.3± 0.9**	0.8± 2.3	-0.8 ±1.5	0.8 ±1.3	-0.2 ±0.3	-0.1 ±0.5	0.2±2.3	-3.9±2.5	-2.1±3.1
[1]	4.3 ±4.4	-2.7± 4.1	-1.7±8.5	-10.3 ±6.6	-14.3±7.6	2.3 ±1.5	0.8 ±1.9	5.0±11.0	0.0±9.9	-6.7±10.8
χ^2	16.20**	1.71ns	51.29**	3.37ns	9.56*	0.02ns	0.01ns	85.67**	33.37**	116.30**
Type of epistasis	C	D	D	D	D	D	C	C	C	D

*, ** significant at 0.05 and 0.01 probability levels, respectively, χ^2- chi square,m- mean, [d]-additive effect, [h]- dominance effect, [i]- additive x additive effect, [j]- additive x dominanceeffect, [1]- dominance x dominance type of genic interaction, D = Duplicate type of epistasis; C = Complementary type of epistasis.

Table.5 Genetic parameters and components of variance for characters studied in HB1307 x Misrach barley cross.

Variances	DH	DM	PH	Lodg1	Lodg2	PhT	SPL	NK/Spk	TKW	GY/Pl
D	-2.6	0	-10.63	-4.00	5.33	0.11	0.06	15.3	-7.95	4.22
H	-2.03	1.68	-0.73	12.3	9.65	0.23	-0.10	-13.67	7.69	-59.76
E	3.33	0.58	5.83	0.25	0.25	0.05	0.28	7.75	5.09	19.8
F	0	0	-2.67	+4.00	-0.67	+0.13	+0.21	+4.00	-8.48	+9.48
$(H/D)^{1/2}$	+0.88	-	+0.26	-1.75	+1.35	+1.45	-1.29	-0.95	-0.98	-3.76
$F/\sqrt{HxD}$	0	0	-0.96	-0.57	-0.09	+0.82	-2.7	-0.28	+1.10	-0.60
h^2b	0.582	0.74	0.661	0.985	0.984	0.872	0.364	0.789	0.754	0.764
h^2n	0.327	0	0.618	0.241	0.350	0.282	0.136	0.417	0.384	0.05
ΔG	0	0	0.42	0.66	3.85	0.10	0.06	10.31	2.40	0.72
ΔG%	0	0	423.5	120.0	832.0	14.6	15.5	6916.2	1540.5	308.6

D= additive variance, H= dominance variance, E= environmental variance, $(H/D)^{1/2}$ = average degree of dominance, F= correlation between D and H over all loci, h^2b = broad sense heritability, h^2n = narrow sense heritability, ΔG = genetic advance, ΔG% = genetic advance as percentage of F_2 mean.

The results of diallel analysis and generation mean analysis revealed the importance of allelic and non-allelic interaction of genes controlling the inheritance of desirable characters for lodging resistance and yield.

Grace and Sabini contained useful fixable additive alleles for reducing plant height and increased tolerance to lodging; While HB42 and HB1307 had fixable additive alleles for high yield. The finding suggests more additive effects of the genes have been expressed lodging tolerance in barley.

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