Genetic Analysis of Agronomic Traits in Barley (*Hordeum vulgare* L.)Landrace Lines under Drained and Waterlogged Conditions

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Abstract

Estimates of genetic parameters are useful to predict the breeding values of genotypes that will help to make effective crosses. This study was undertaken to estimate genetic parameters and determine the breeding values of barely landrace lines waterlogged and drained conditions. Two sets of experiments each consisting of five landrace lines and 10 F_1 crosses generated in diallel mating were established in a greenhouse at the University of the Free State, South Africa. Analysis of variance showed significant variations among genotypes for most studied traits under drained experiment but non-significant variation for most traits under waterlogging. As compared to the drained experiment, waterlogging reduced grain yield and number of productive tillers; and delayed days to heading and maturity. General combining ability (GCA) mean squares were significant for most traits, whereas mean squares for specific combining ability (SCA) were significant only for few traits. Additive gene action was found to be important for days to heading and maturity while both additive and non-additive gene effects were important in conditioning spike length under both drained and waterlogged conditions. Under drained conditions, only additive gene action was important for seeds spike^{-1} and grain yield spike^{-1}, while both additive and non-additive gene effects were important in conditioning grain yield. The values of estimates of genetic parameters for yield and yield components (except spike length) were very low under waterlogged conditions, indicating adverse effect of waterlogging stress on the expression of genetic effects. Among the parental lines, Feres Gama(37) and 1153(28) showed high positive GCA effects for yield and yield components under drained condition Moge(07), 1182(44) and 1153(82) showed desirable GCA effects for early maturity. These parents could be extensively used in future breeding programs to develop crosses with higher grain yield and desirable agronomic traits. None of the inbred lines showed desirable GCA effects for grain yield and most other yield related traits under waterlogged condition, indicating the need for further research with increased number of lines to identify the ones with better combining ability.

Key words: Barely, GCA, genetic analysis, lines, landraces, SCA

Introduction

Pure line selection within locally adapted landraces is one of the easiest and cheapest methods of improvement (Ceccarelli and Grando, 1996; Lakew *et al.*, 1997). However, pure line selection is only a short-term strategy and, in the long-term, the best pure lines should be used in the crossing program either with other pure lines from landraces or with non-landrace material to cope with the unpredictable variability of abiotic stresses (Ceccarelli and Grando, 1996). To this effect, estimates of genetic parameters for quantitative traits are very useful since they provide information on the inheritance of traits and help to identify appropriate breeding methods (Muehlbauer *et al.*, 1995).

An important point in estimating combining ability and genetic parameters is the environment in which the test of the progenies was carried out (i.e. stress vs optimum). Gouis *et al.* (2002) reported differences in general combining ability effects of parents when evaluated under low and high levels of nitrogen and concluded that results obtained at a high N level would not allow identification of parents and that specific experiments at low N level will be necessary. The assumption that in high yielding conditions there is more efficient control of environmental variation, better expression of genetic differences, and hence higher heritabilities than in stress environments (Roy and Murty, 1970) was also argued and it has been shown that it is not always true that heritability is higher in high-yielding than in low-yielding environments (Singh *et al.*, 1993; Ceccarelli, 1996).

In Ethiopia, barley crossing program was started in 1968; however, information on combining abilities and genetic variances from a landrace based crossing is not available. Lack of such information will not permit the identification of superior varieties to be used as parents for hybridisation and cross-combinations likely to yield desirable segregates (Witcombe and Virk, 2001). The objectives of this study were therefore to (i) estimate genetic parameters from diallel crosses involving five pure lines derived from landraces and (ii) to determine the breeding value of the parents under contrasting environments (waterlogged vs. drained) so that the progeny performance from crosses involving the best parents could be predicted.

Materials and Methods

Plant materials

Five parents (Feres Gama(37), Feleme(68), 1153(28), 1182(44) and Mage(07) were selected based on their agronomic attributes and differences in response under waterlogging stress. Feres Gama(37) has long spikes (7.8 cm to 8.4 cm), white seeds, gives very good yield but it is late maturing and takes about 88 to 91 days to heading and 142-145 days to mature. Feleme(68) has relatively short spikes (6.5 cm), white seeds, reaches heading in about 80 to 83 days and matures in about 124 days. Line 1153(28) is an early maturing landrace comparable to Feleme(68) and has comparably long spikes to Feres Gama(37) with black seed colour. Mage(07) is a random selection from a local cultivar grown predominantly on low-lying "guie" fields where waterlogging due to excessive rainfall in the main rain season is a problem in

north Shewa. It is early in heading and maturity, has irregular spikes with dull white seeds and has good early vegetative growth. Line 1182(44) is a pure line landrace characterized by very short and dense spike, stiff straw and is early as compared to Feres Gama(37).

The five landrace lines were crossed in all possible combinations (excluding reciprocals) to generate 10 F_1 progenies. Crossing was done in an open field at Holetta Research Centre in 2001 by hand emasculation with pollination by the approach-cross method.

Experimental design

Two sets of experiments each consisting 15 genotypes (five parents and the 10 F_1s) were planted in a greenhouse. In set I each parent and crosses were planted in 3 litre size pots perforated at the bottom. Six seeds were planted per pot and later thinned to four uniformly germinated seedlings. The experimental layout was a randomised complete block in four replications. Fertilizer was applied at a ratio of 2:3:2 for N: P: K, respectively, that is, at the rate of 378.4 mg N, 567.6 mg P and 378 mg K per pot. Pots were watered to field capacity every day for normal growth and development of plants. Insecticide was sprayed, whenever necessary, to control aphids. Set II experiment was conducted with the same parents and crosses to evaluate the response of genotypes to waterlogging stress. Seedlings were germinated in a similar manner to set I experiment. When seedlings reached three-leaf stage, pots with seedlings were put inside other larger pots. The larger pots were filled with water until the water level in the pots containing the seedlings reached nearly 10mm above the soil surface. This level of water was maintained for three weeks,

and afterwards the excess water was drained and plants were allowed to grow until maturity without waterlogging stress.

Measurements

Days to heading, days to maturity, plant height, spike length, number of seeds spike^{-1}, total productive heads per pot, grain yield per main spike, average kernel mass of main spikes (grain yield per main spike divided by the total number of seeds per main spikes) and grain yield per pot were recorded from the parents and F_1 crosses.

Statistical methods

Analysis of combining ability

Analysis of combining ability was carried out according to Griffing's (1956b) method II (parents and F_1 progenies without reciprocals) and Model I (where genotypes are considered as fixed effects). It may be assumed that the landrace lines used as parents are random selections from populations and thus Model II was used for analysis of gentic parameters. From statistical geneticists point of view, variance of combining ability can be considered as population parameters (Sprague, 1966). This inform will help to predict the gene action within a given set of population from which the inbred lines under study were selected. The analyses of combining abilities were performed using the Agrobase 2000 computer program.

The ratio of mean square components associated with GCA and SCA effects were calculated according to Baker (1978) to estimate the relative importance of GCA in explaining the importance of additive vs non-additive

gene effects. Statistical testing for GCA effects of parents was done as standard error of the GCA (SEgi) x 1.96 and differences between parents for GCA effects was done as (SEgi-gj) x 1.96 at 5% probability level. Testing the significance of differences for SCA effects of crosses with one common parent and no parent in common was done as SEij-ik x 1.96 and SEij-kl x 1.96, respectively.

Estimation of variance components and heritability

Variance of GCA (δ^2gca) was calculated as *(MSgca - MSsca)/n+2* while variance of SCA (δ^2sca) was computed as MSsca-MSe where MSgca, MSsca and MSe stand for mean squares of the GCA, SCA, and error, respectively, and n is number of parents (Griffing, 1956b). According to Grifing (1956b), additive genetic variance (δ^2_A) is twice the GCA variance ($2\delta^2$gca) while the dominance variance (δ^2_D) is equivalent to the SCA variance (δ^2sca). The total genetic variance (δ^2_g) was calculated as $\delta^2_{g\,=\,}\delta^2_A + \delta^2_D$ and the phenotypic variance (δ^2_p) = $\delta^2_g + \delta^2_e$. The GCA and SCA effects were also used to calculate the estimates of GCA and SCA variances associated with each parent, $\delta_{\hat{g}i}^2$ and $\delta_{\hat{s}i}^2$, respectively, according to the method suggested by Griffing (1956b).

Determination of heritability is one of the first objectives in the genetic study of a metric character. The extent to which individuals' phenotypes are determined by the genotypes is called broad sense heritability *(h²b)* and is expressed as the ratio of genotypic variance *(δ^2_g)* to phenotypic variance *(δ^2_p)*; hence *h²b=δ^2_g/δ^2_p*. The extent to which phenotypes are determined by the genes transmitted from the parents is called narrow sense heritability *(h²n)*

and is obtained as the ratio of additive genetic variance (δ^2_A) to phenotypic variance *(δ^2_p)*; and expressed as *h²n = δ^2_A/ δ^2_p* (Falconer and Mackay, 1996).

Results and Discussion

Agronomic performance of F1 crosses and parents

Waterlogging remarkably delayed days to heading by 11 to 26 days and on average by 18 days (Tables 1 and 2). The effect was very pronounced on all progenies involving the susceptible parent Feres Gama(37). Accordingly, the difference in days to heading under drained and waterlogged conditions of crosses involving this parent was very high. The mean days to heading pooled over parents and progenies was 82 days under drained conditions (Table 4) while it was 99 days under waterlogged conditions (data not shown). The effect was comparatively less on days to maturity. The mean difference in maturity of progenies and parents between control and waterlogged treatments was almost one week.

Although plants under waterlogged conditions had delayed heading and maturity days, they achieved almost equivalent plant height with the plants in the drained experiment. This was probably because under waterlogged conditions productive tillers were reduced significantly and the surviving tillers might have taken advantage of reduced competition effects for available nutrients that allowed recovery and growth maintenance. Spike length, number of seeds spike⁻¹ and grain yield spike⁻¹ of the waterlogged plants was comparable and even in some cases greater than that of the plants under drained experiment. There was marked difference for grain

yield, and this was expected because waterlogged and drained plants had apparent differences in total productive tillers. The difference in grain yield spike^{-1} between the drained and waterlogged plants of Feres Gama(37) was wider (1.24g spike^{-1}) than for Mage(07) that showed a mean difference of only 0.21 g spike^{-1}. Similarly, number of seeds spike^{-1} and grain yield pot^{-1} of the susceptible Feres Gama(37) decreased by 22 and 3.84 g, respectively while the corresponding values for the tolerant Mage(07) was only 5 and 2.0 (Tables 1 and 2) which indicated differences in the relative sensitivity of the landraces to waterlogging stress. All crosses involving the tolerant parent, Mage(07) had higher grain yield spike^{-1} and grain yield pot^{-1} under waterlogged conditions than all crosses involving the parent Feres Gama(37). The reverse was true under free drainage conditions. This indicated differences between landraces and their progenies in the expression of their genetic potential under drained and waterlogged situations.

Combining ability effects

Under waterlogged conditions, the analysis of variance showed significant GCA mean squares for days to heading, days to maturity, and spike length (Table 3) implying the importance of additive genetic mechanisms in determining these characters. Consistent with the waterlogging treatment, GCA for days to heading, days to maturity, spike length, number of seeds spike^{-1} and grain yield spike^{-1} were significant under drained conditions. Both GCA and SCA mean squares were highly significant for spike length under both treatment levels, suggesting the importance of both additive and dominant gene actions for this character. However, a GCA/SCA ratio higher than unity demonstrates that this character is predominantly under the control of additive gene action. In the drained treatment, grain yield appeared to be determined both by additive and dominant gene action as observed from the low GCA/SCA ratio.

Similar combining ability studies in barley (Bhatnagar and Sharma, 1997; Hanifi and Gallais, 1999) indicated that GCA effects are more important in determining grain yield and yield components in environments free of stress. Phogat *et al*. (1995b), however, reported that both GCA and SCA effects are important for yield and yield components. Based on the result from the drained experiment, when the SCA effects were not significant, the performance of the cross progenies could be predicted based on GCA estimates of the parents because the parents with higher GCA estimates would be expected to produce superior progenies. In this regard Feres Gama(37) and 1153(28) were found to be good combiners (Table 2). Other investigators reported, however, that crosses between good general combiners would not always result in good F_1 combinations (Wells and Lay, 1970; Shrivastava and Seshu, 1983).

The patterns of GCA effects of parents for days to heading and days to maturity are similar for the drained (Table 1) and waterlogged (Table 2) treatments in that the three early lines, Mage(07), 1182(44) and 1153(28), had negative GCA effects for days to heading and maturity, whereas Feres Gama(37) had positive GCA effects under both conditions (Tables 1 and 2). Earliness is a desirable feature and

Table 1. Mean performances and general combining ability (GCA) effects of five landrace lines of barely evaluated in diallel crosses for grain yield and agronomic traits under drained condition.

Parents	DHE		DMA		PLH		SPL		NS/SP		GY/SP		GY (g/pot)	
	Mean	GCA	Mean	GCA	Mean	GCA	Mean	GCA	Mean	GCA	Mean	GCA	Mean	GCA
F.Gama(37)	102a	7.636**	152a	5.943**	89	2.957	7.1a	0.619**	44a	6.378**	2.27a	0.352**	7.88	0.305
Feleme(68)	81b	-0.900	138b	1.014	82	-2.293	5.5c	-0.252**	28c	-3.121**	1.38b	-0.187**	8.76	-0.016
Mage(07)	77b	-2.150**	132c	-2.628**	83	-0.829	5.7c	-0.152	27c	-3.086*	1.47b	-0.180**	7.32	-0.492
1182(44)	75b	-3.436**	137bc	-2.378**	82	0.386	4.2d	-0.464**	28c	-0.978	1.44b	-0.079	6.29	-0.509
1153(28)	81b	-1.150	132c	-1.950*	82	-0.221	6.3b	0.251**	37b	0.807	2.00a	0.095	9.22	0.680*
LSD$_{0.05}$	5.7		5.2		NS		0.47		6.2		0.29		NS	
CV(%)	7.1		3.9		6.0		8.6		19.9		17.8		18.9	
SE(gi)		1.579		1.709		NS		0.163		2.366		0.122		0.53
SE(gi-gj)		2.498		2.703		NS		0.258		3.742		0.192		0.847

*=significant at P$\leq$0.05, **=significant at P$\leq$0.01, respectively, CV= coefficient of variation, DHE=days to heading, DMA= days to maturity, GCA=general combining ability, GY=grain yield, GY/SP=grain yield spike[-1], LSD= least significant difference, NS/SP=number of seeds spike[-1], PLH=plant height, SE= standard error and SPL=spike length.

Table 2. Mean performances and general combining ability (GCA) effects of five landrace lines of barely evaluated in diallel crosses for grain yield and agronomic traits under waterlogged condition.

Parents	DHE		DMA		PLH		SPL		NS/SP		GY/SP		GY(g/pot)	
	Mean	GCA	Mean	GCA	Mean	GCA	Mean	GCA	Mean	GCA	Mean	GCA	Mean	GCA
F.Gama(37)	116a	8.207**	165a	8.214**	88	1.064	6.3b	0.296**	22	-3.028	1.04	-0.222	4.03	-0.674
Feleme(68)	95bc	-1.686	144b	-2.571**	79	-2.007	6.2b	0.039	38	1.614	1.80	0.023	7.05	0.106
Mage(07)	91c	-3.543**	144b	-1.393	79	1.957	6.1b	0.078	32	3.043	1.69	0.185	5.32	0.442
1182(44)	97b	-1.078	142b	-2.107*	81	-0.257	3.9c	-0.607**	26	-0.528	1.13	-0.077	4.64	-0.228
1153(28)	96bc	-1.900	145b	-2.143*	82	-0.757	6.9a	0.193	30	-1.100	1.73	0.091	5.56	0.354
LSD$_{0.05}$	5.8		4.3		NS		0.48		NS		NS		NS	
CV(%)	6.2		3.0		7.7		8.6		35.0		33.5		44.0	
SE(gi)		2.333		1.748		NS		0.194		NS		NS		NS
SE(gi-gj)		3.688		2.764		NS		0.307		NS		NS		NS

*=significant at P$\leq$0.05, **=significant at P$\leq$0.01, respectively, CV= coefficient of variation, DHE=days to heading, DMA= days to maturity, GCA=general combining ability, GY=grain yield, GY/SP=grain yield spike[-1], LSD= least significant difference, NS/SP=number of seeds spike[-1], PLH=plant height, SE= standard error and SPL=spike lengt.

crosses involving these lines are expected to provide on average early heading and maturing progenies regardless of the stresses of waterlogging. Mage(07) and 1182(44) had negative GCA effects for yield and yield components, and therefore, are not the desired parents if the aim is to improve grain yield for environments where waterlogging is not a problem. However, yield stability is more important than high grain yield under stress environments and Mage(07) may be the preferred parent because of its consistently higher positive GCA effects for yield and yield components than all other parents under waterlogged conditions (Table 2). However, the non-significant GCA mean square values for yield and yield components except spike length put the importance of this line in question. Under the free drainage environment, among the early lines, 1153(28) had positive GCA effects for all yield components and implied the possibility of combining earliness and high grain yield. Feres Gama(37), on the other hand, is very late compared to the other three lines and accordingly demonstrated positive GCA effects for days to heading and maturity under both environments. Moreover, the GCA effects of Feres Gama(37) is higher than GCA effects of the other parental lines in all cases and the effects were significant for all characters observed under drained conditions except for grain yield (Table 1).

Generally, under drained conditions, Feres Gama(37) and 1153(28) had higher positive GCA effects for yield and yield components (spike length, number of seeds spike^{-1} and grain yield spike^{-1}) (Table 1). These lines were found to be good combiners for yield and yield components; and accordingly, the cross between these two parents gave the highest mean spike length, grain yield spike^{-1} and grain yield than all the other crosses. This cross is also among the top in number of seeds spike^{-1} in the drained experiment (Table 4). GCA effects of 1153(28) for number of seeds spike^{-1} and grain yield spike^{-1} were not significant implying that this parent were not good combiners as that of Feres Gama(37) for these characters. The difference between the GCA effects of the two parents for spike length is significant denoting that both parents are desirable, whereas the difference in GCA effects for grain yield is not significant under waterlogged conditions.

Although Feres Gama(37) had significant positive GCA effects for days to heading and maturity, under the drained experiment, all crosses with this parent showed negative SCA effects for days to heading and maturity except that of Feres Gama(37) x Mage(07) and Feres Gama(37) x 1153(28) (Table 4). For spike length and grain yield both GCA and SCA mean square values were significant in the drained experiment (Table 2). High positive SCA effects for spike length was observed in crosses of Feres Gama(37) x 1182(44), Feres Gama(37) x 1153(28) and Mage(07) x 1182(44). Higher SCA effects for grain yield were also observed in these three crosses and 1182(44) x 1153(28) (Table 4). In this set experiment, some of the crosses which showed significant positive SCA effects for spike length (Feres Gama(37) x 1182(44) and for grain yield (Feres Gama(37) x 1182(44) and 1182(44) x 1153(28) involved one good and another poor general combiner parent for these characters. Such crosses would be expected to produce desirable transgressive segregants if the additive genetic system present in the parents with desirable GCA, (1153(28) and Feres

Table 3. Combining ability analysis of five barley landrace lines evaluated under drained (D) and waterlogged (WL) conditions in a greenhouse.

Source of variation	Expt.	DF	DHE	DMA	PLH	SPL	NS/SP	GY/SP	GY
GCA	drained	4	134.511***	92.253***	26.051	1.314***	107.730***	0.361***	1.852*
	WL	4	153.167***	148.853***	16.854	0.877***	39.421	0.173	1.467
SCA	drained	10	10.219	12.680	7.628	0.381***	20.401	0.037	1.497*
	WL	10	10.294	11.155	19.786	0.582***	30.042	0.083	2.040
Residual	drained	42	5.684	6.656	8.203	0.061	12.758	0.034	0.654
	WL	42	12.397	6.961	13.864	0.086	19.252	0.066	1.528
GCA/SCA	drained		13.16	7.270	3.415	3.450	5.280	9.750	1.240
	WL		14.88	13.940	-	1.507	-	2.080	-

*=significant at $P \leq 0.05$, ***=significant at $P \leq 0.001$, respectively, DF=degrees of freedom, DHE=days to heading, DMA= days to maturity, Expt.=experiment, GCA=general combining ability, GY=grain yield, GY/SP=grain yield spike[-1], NS/SP=number of seeds spike[-1], PLH=plant height, SCA=specific combining ability, SPL=spike length and WL=waterlogged.

Gama(37), and complementary non-additive effects of the F_1 crosses contributed to the improvement of desirable attributes. Under waterlogging conditions, only spike length had significant SCA mean squares and the highest positive SCA effects were noted for crosses Feres Gama(37) x Feleme(38), Mage(07) x 1182(44) and Feres Gama(37) x 1182(44). These crosses also showed higher mean spike lengths than all the other F_1 crosses.

Estimates of genetic parameters

Results from the drainage experiment elucidated that additive genetic variance (δ^2_A) was very high for all characters except for grain yield in which dominance genetic variance (δ^2_D) was found to be greater than that of δ^2_A, whereas spike length showed comparable values of δ^2_A and δ^2_D (Table 5). Spike length was the only character that displayed significant SCA mean squares; and hence, relatively higher δ^2_D. However, the additive genetic variance was lower than the dominance variance (δ^2_D) under waterlogged conditions (Table 6). The fact that the GCA: SCA ratio was relatively higher may lead to the assertion that additive gene action is more important than the non-additive portion in the inheritance of this character. It is erroneous, however, to conclude that additive or non-additive gene action is predominant on the basis of relative magnitude of significant GCA and SCA mean square values without considering the respective GCA and SCA variances. This is true because the variance of general combining ability is equal to the additive variance and the variance of specific combining ability is equal to the non-additive variance (Falconer and Mackay, 1996). Hence in view of this, it may be assumed that spike length is not under the control of

Table 4. Mean agronomic performance and specific combining ability (SCA) effects of F_1 crosses of barley landrace lines evaluated under drained conditions in a greenhouse.

Crosses	DHE		DMA		SPL(cm)		NS/SP		GY/SP(g)		GY (g/pot)	
	Mean	SCA	Mean	SCA	Mean	SCA	Mean	SCA	Mean	SCA	Mean	SCA
F.Gama(37) x Feleme(68)	84	-4.369	141	-3.190	6.5	-0.107	42	2.976	2.21	0.164	9.15	-0.019
F.gama(37) x Mage(07)	87	-0.369	141	0.952	6.6	-0.107	44	4.190	2.01	0.087	9.29	0.631
F.gama(37) x 1182(44)	81	-5.083	136	-4.298	7.1	0.682*	47	5.583	2.48	0.332	10.25	1.598*
F.Gama(37) x 1153(28)	88	-0.369	142	1.274	7.6	0.439*	41	-2.702	2.34	0.020	10.82	0.983
Feleme(68) x Mage(07)	81	2.167	137	1.131	5.6	-0.285	33	2.690	1.55	0.041	8.65	0.672
Feleme(68) x 1182(44)	78	0.452	133	-3.119	6.2	0.603*	31	-0.667	1.64	0.028	7.61	-0.750
Feleme(38) x 1153(28)	81	0.917	143	6.702	6.6	0.311	33	-0.952	1.65	0.006	7.90	0.355
Mage(07) x 1182(44)	79	2.702	132	-0.274	6.5	0.853*	33	0.798	1.64	0.018	8.55	0.700
Mage(07) x 1153(28)	75	-3.833	130	-2.905	6.5	0.061	31	-2.488	1.73	-0.065	8.14	-0.899
1182(44) x 1153(28)	79	1.452	132	-1.405	6.2	0.125	43	6.905	1.97	0.169	10.56	1.540*
Mean	82		137		6.3		36		1.85		8.83	
LSD$_{0.05}$	6.8		8.6		0.7		10		0.54		2.46	
LSD$_{0.01}$	9.1		11.5		0.9		14		0.72		NS	
CV (%)	5.82		4.4		7.8		19.8		19.90		19.40	

*=significant at P$\leq$0.05, CV= coefficient of variation, DHE=days to heading, DMA= days to maturity, SCA=specific combining ability, GY=grain yield, GY/SP=grain yield spike[-1], LSD= least significant difference, NS/SP=number of seeds spike[-1] and SPL=spike length.

additive gene action under waterlogging stress since the GCA variance (δ^2gca) is lower than SCA variance (δ^2sca) suggesting low genetic advance by selection for this character.

Under drained environments, the predominant role of non-additive gene action in the inheritance of grain yield was reported by Kudla and Kudla (1995); and Bouzerzour and Djakoune (1997). Previous investigators reported the importance of additive gene action in determining grain yield spike^{-1} and heading date (Kudla and Kudla, 1995; Esparza-Martinez and Foster, 1998), and number of seeds spike^{-1} (Bouzerzour and Djakoune, 1997) under environments free of waterlogging stress. In this study, although grain yield appeared to be governed both by both additive and non-additive gene actions under drained conditions, most yield components were found to be under the effects of additive gene actions. Contrary to this finding, other researchers reported the importance of both additive and non-additive gene actions for grain yield and yield components (Phogat et al., 1995a) and for days to heading and maturity (Singh and Singh, 1990a). Under waterlogging stress, the additive genetic variance (δ^2_A) for days to heading and days to maturity were very high as compared to the respective dominance genetic variance (δ^2_D) (Table 6), indicating the importance of additive gene actions in the expression of these characters, which was consistent with the results from the drained experiment.

The waterlogged experiment was generally characterized by negative estimates of genetic parameters that were not the case with data from the drained experiment. Hogarth (1971) indicated that negative estimates of genetic parameters are meaningless, but they should be presented for illustrative purpose, the values being taken as zero, or in order to contribute to the accumulation of knowledge (Dudley and Moll, 1969). Maluf *et al*. (1983) put his notion, however, that negative value of genotypic variance is most likely the result of low magnitude of genotypic variance in relation to variance of error (δ^2_e) and not because of the non-existence of genetic variation; or because of situations where characters in the parental means are very close so that variance estimates in the hybrid population will be close to zero (Haddad, 1982). Hence, the resulting negative heritability values shall be considered as very low rather than zero.

Lack of precision in an experiment was also considered as a major factor for negative variances. Comstock and Moll (1963) showed that well replicated experiments in time and space would improve precision or repeated experimentation involving the same character in related populations will give estimates, which when averaged, approach a true value (Dudley and Moll, 1969). However, Hogarth (1971) obtained negative estimates of genetic parameters despite the high precision in his experiment as judged by the coefficient of variation and he coined the issue with his view that it is a major problem in quantitative genetic studies. Considering all these views, the negative estimates of genetic parameters observed in this study under waterlogged conditions shall be treated with caution.

Table 5. Estimates of genetic parameters for seven agronomic characters in a diallel cross of barley landrace lines evaluated under drained conditions in a greenhouse.

Character	GCA	SCA	δ^2_e	δ^2_{gca}	δ^2_{sca}	δ^2_A	δ^2_D	δ^2_g	δ^2_p	h^2_b	h^2_n	PR
DHE	134.51	10.21	5.68	18.40	4.53	36.80	4.53	41.34	47.02	0.88	0.78	0.89
DMA	92.25	12.68	6.65	12.22	6.02	24.45	6.02	30.48	37.13	0.82	0.66	0.80
PLH	26.05	7.62	8.20	2.54	-0.57	5.09	-0.57	4.52	12.72	0.35	0.40	1.13
SPL	1.31	0.38	0.06	0.17	0.32	0.35	0.32	0.67	0.73	0.92	0.48	0.53
NS/SP	107.73	20.40	12.75	13.56	7.64	27.13	7.64	34.77	47.53	0.73	0.57	0.78
GY/SP	0.36	0.03	0.03	0.04	0.00	0.09	0.00	0.09	0.13	0.71	0.72	0.97
GY	1.85	1.49	0.65	0.17	0.84	0.34	0.84	1.18	1.83	0.64	0.19	0.29

DHE=days to heading, DMA= days to maturity, GCA=general combining ability, GY=grain yield, GY/SP=grain yield spike^{-1}, PHL=plant height, NS/SP=number of seeds spike^{-1}, PR= predictability, SCA=specific combining ability, and SPL=spike length, h^2_b= broad sense heritability, h^2_n= narrow sense heritability, δ^2_A= additive variance, δ^2_D= dominance variance, δ^2_e= error variance, δ^2_g= genotypic variance, δ^2_{gca}=GCA variance, δ^2_p= phenotypic variance and δ^2_{sca}= SCA variance.

Table 6. Estimates of genetic parameters for different agronomic traits in a diallel cross of barley landrace lines evaluated under waterlogged condition in a greenhouse.

Variable	MSgca	MSsca	$\delta^2 e$	$\delta^2 gca$	$\delta^2 sca$	δ^2_A	δ^2_D	$\delta^2 g$	$\delta^2 p$	$h^2 b$	$h^2 n$	PR	GCA:SCA
DHE	153.167***	10.294	12.397	20.410	-2.103	40.82	-2.10	38.72	51.11	0.76	0.79	1.05	14.88
DMA	148.853***	11.155	6.961	19.671	4.194	39.34	4.19	43.54	50.49	0.86	0.78	0.90	12.34
PLH	16.854**	19.786	13.864	-0.419	5.922	-0.84	5.92	5.08	18.95	0.27	-0.04	-0.16	-
SPL	0.877***	0.582***	0.086	0.042	0.496	0.08	0.49	0.580	0.67	0.87	0.13	0.15	1.51
NS/SP	39.421	30.042	19.252	1.339	10.790	2.68	3.07	5.75	25.00	0.23	0.11	0.19	-
GY/SP	0.173*	0.083	0.066	0.013	0.017	0.026	-2.10	-2.08	-2.01	1.03	-0.01	0.60	2.08
GY	1.467	2.040	1.528	-0.082	0.512	-0.16	0.02	-0.15	1.38	-0.10	-0.12	-0.47	-

DHE=days to heading, DMA= days to maturity, GCA=general combining ability, GY=grain yield, GY/SP=grain yield spike[-1], PHL=plant height, NS/SP=number of seeds spike[-1], PR= predictability, SCA=specific combining ability, and SPL=spike length, $h^2 b$= broad sense heritability, $h^2 n$= narrow sense heritability, δ^2_A= additive variance, δ^2_D= dominance variance, $\delta^2 e$= error variance, $\delta^2 g$= genotypic variance, $\delta^2 gca$=GCA variance, $\delta^2 p$= phenotypic variance and $\delta^2 sca$= SCA variance.

Conclusions

Feres Gama(37) and 1153(28) equally showed desirable GCA effect for grain yield and yield components under the drained experiment. Hence, it can be concluded that Feres Gama(37) and 1153(28) were good combiners that could be used in future crossing program aimed at improving grain yield and yield components for environments free of waterlogging problems. Non-significant variations were observed for genotypes, GCA and SCA effects for most traits under waterlogged conditions, indicating the adverse effects of expression of these characters and their genetic effects under stressed environments. Estimates of genetic variances and heritability values reported in this article are from experiments conducted in only in one year. The values are, therefore, likely to be biased upwards due to confounding effects. It is desirable to conduct similar experiment across locations and years to come up with more reliable inferences. Nevertheless, the findings of this study shouldn't have to be underestimated as it provided initial information on agronomic performance and genetic expression of traits in barely under drained and waterlogged environments.

Acknowledgement

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