Global Journal of Science Frontier Research
Agriculture and Veterinary Sciences
Volume 13 Issue 3 Version 1.0 Year 2013
Type : Double Blind Peer Reviewed International Research Journal
Publisher: Global Journals Inc. (USA)
Online ISSN: 2249-4626 & Print ISSN: 0975-5896

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By Alemayehu Assefa & M.T. Labuschagne
Ethiopian Institute of Agricultural Research

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GJSFR-D Classification : FOR Code: 070199

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Alemayehu Assefa[α] & M.T. Labuschagne[σ]

Abstract - Estimates of genetic parameters are useful since they provide information on the inheritance of characters and help to predict the value of crosses. If the value of crosses cannot be predicted, many crosses need to be made which results in each cross having a small population size, fewer progenies in later generations and a lower probability of recovering good genotypes from each cross. The objectives of this study were therefore i) to estimate genetic parameters from diallel crosses involving five inbred lines: Feres Gama(37), Feleme(68), Mage(07), 1153(28) and 1182(44) that vary for different agronomic characters and ii) to determine the breeding value of the parents so that the progeny performance from crosses involving the best parents could be predicted. Data for agronomic characters were obtained from parents and F1 progenies evaluated in a greenhouse under waterlogged and free drainage conditions. The results highlighted the importance of additive gene action for spike length, number of seeds spike^{-1} and grain yield spike^{-1} under free drainage conditions and for days to heading and days to maturity at both treatment levels. Both additive and non-additive gene action were important in the control of grain yield under free drainage conditions. By contrast, estimates of genetic parameters for yield and yield components (except spike length) were very low or negative under waterlogged conditions. Among the parents, Feres Gama(37) and 1153(28) contributed the highest positive GCA effects and comparable SCA variances for yield and yield components under free drainage conditions. Hence, these parents shall be tested thoroughly in order that maximum use of their superior combining ability can be made in future crossing programs for environments free of waterlogging stress. A separate crossing and selection program is suggested for the respective environmental conditions if resources permit.

I. Introduction

Pure line selection within locally adapted germplasm is one of the easiest and cheapest methods of improvement (Ceccarelli & Grando, 1996; Lakew et al., 1997). However, pure line selection within landraces 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 & 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 (Dudley & Moll, 1969; Muehlbauer et al., 1995). Genetic variance can be subdivided into additive, dominance and epistatic effects of genes (Muehlbauer et al., 1995; Falconer & Mackay, 1996). The additive component of genotypic variance is very important because it is the chief source of resemblance between relatives, and also the chief determinant of observable genetic properties of the population and of the response of the population to selection (Dabholkar, 1992; Falconer & Mackay, 1996). Therefore, the effectiveness of selection is based on the utilization of additive gene effects (Sprague, 1966) and should be utilized as fully as feasible before undertaking an expensive and time consuming crossing program.

Methods are available for the partitioning of either means or variances that provide information as to the presence or absence of genetic variability and, in addition, provide information on the type of gene action involved (Sprague, 1966; Fehr, 1987; Dabholkar, 1992). Estimation of additive and dominance variances can be obtained through use of a nested design or from diallel crosses (Sprague, 1966). Information from diallel crosses can be used to characterize crossing relationships among a group of varieties or lines with the goal of identifying crosses which would be expected to be good source material for selections (Matzinger, 1963). If the variance is primarily of the additive type, that is, if the parents have a high degree of general combining ability, superior selfed families can be identified on the basis of their crossbred performance and be incorporated into a varietal development program (Baker, 1978).

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

Author α : Ethiopian Institute of Agricultural Research, Addis Ababa Ethiopia. E-mail : a_assefa@yahoo.com
Author σ : University of Free state, Republic of South Africa. E-mail : labuscm.sci@mail.uovs.ac.za

Global Journal of Science Frontier Research (D) Volume XIII Issue III Version I Year 2013

more efficient control of environmental variation, better expression of genetic differences, and hence higher heritabilities than in stress environments (Roy & 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, 1994, 1996). Shibin et al. (1996) for instance, observed high heritability (71.5 %) of waterlogging tolerance from analysis of F1 diallel crosses of common wheat which negates the view that heritability is low in stress environments. Moreover, it was noted that measurements made on the same genotypes in two different environments should be regarded as separate and the relative effectiveness of selection strategies depends on the genetic correlations between performances in the two contrasting environments (Falconer, 1981). Hence, the genetic correlation coefficient has to be considered before deciding which the optimum environment for selection is (Ceccarelli, 1994) because partial differences in alleles that control high grain yield in high-yielding and low-yielding environments were also indicated (Ceccarelli et al., 1992).

In Ethiopia, although crossing program started early in 1968, it was not designed to allow estimates of combining abilities and genetic variances from a landrace based crossing programs so that information in this regard is not available. The lack of such information will not permit the identification of superior varieties to be used as parents for hybridisation and also pinpoint cross-combinations likely to yield desirable segregates (Dabholkar 1992; Witcombe & Virk, 2001). The objectives of this study were therefore i) to estimate genetic variances, heritability and genetic correlation of characters from crosses between adapted inbred barley landrace lines selected based on their merits and ii) to determine the breeding value of the parents under contrasting environments (free drainage vs waterlogged) so that the progeny performance from crosses involving the best parents could be predicted.

II. Materials and Methods

a) 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 well compared to Feres Gama(37).

b) Crossing

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.

c) Experimental Design

Two sets of experiments each consisting the five parents and the 10 F_{1s} were set up in a greenhouse. In set I the parents and the crosses were planted in 3 litre size pots perforated at the bottom. Six seeds were planted per pot and thinned later to four uniformly germinated seedlings per pot. The experimental layout was a randomised complete block in four replications. Fertilizer (2: 3: 2 (22) of N: P: K) was applied at the rate of 378.4mg/pot N, 567.6mg P and 378mg K. 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 their response to waterlogging stress. Seedlings were germinated in a similar manner to set I experiment. When seedlings reached three-leaf stage, putting the pots with seedlings in other larger sized pots imposed waterlogging. 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 thereafter the excess water was drained and plants were allowed to grow until maturity without the waterlogging stress.

d) 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 F1.

III. Statistical Methods

a) 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 has to be used. This view, however, is not universally shared (Mayo, 1987) and it is only from the statistical geneticists point of view that variance of combining ability can be considered as population parameters (Sprague, 1966). The breeder is more interested in gene action within a given set of selected inbred lines for which inference is going to be made and hence Model I is preferred to Model II for this experiment. Therefore, the statistical analysis method of Griffing (1956b) as detailed for method II Model I was applied. 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 progeny performance. Statistical testing for GCA effects of parents was done as S.E (Gi) x 1.96 and differences between parents for GCA effects was done as S.E (G_i-G_j) x 1.96. Testing the significance of differences for SCA effects of corsses with one common parent was done as S.E (S_{ij}-S_{jk}) x 1.96 and S.E (Sij-Skl) x 1.96 for crosses with no parent in common (Dabholkar, 1992).

b) *Estimation of Variance Components*

Variance of GCA (δ^2gca) was calculated as (*MSgca - MSsca)/n+2* while variance of SCA (δ^2sca) as MSsca-MSe where MSgca, MSsca and MSe stand for mean square of the GCA, SCA, and error, respectively and n is number of parents (Griffing, 1956b). Then, the additive genetic variance (δ^2_A) is twice the GCA variance (2δ^2gca) while the dominance variance (δ^2_D) is the 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).

c) *Estimation of Heritability (h^2)*

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 *(h^2_b)* and is expressed as the ratio the genotypic variance (δ^2_g) to phenotypic variance (δ^2_p). Hence $h^2_b=\delta^2_g/\delta^2_p$. The extent to which phenotypes are determined by the genes transmitted from the parents is called narrow sense heritability *(h^2_n)* and is obtained as the ratio of additive genetic variance (δ^2_A) to phenotypic variance *(δ^2_p)* expressed as $h^2_n = \delta^2_A/\delta^2_p$ (Falconer and Mackay, 1996).

IV. Results and Discussion

a) *Agronomic Performance of F1 and Parents*

Waterlogging remarkably delayed days to heading by 11 to 26 days and on average by 18 days (Table 1). The effect was very pronounced on all progenies involving the susceptible parent Feres Gama (37). Accordingly, the difference in days to heading under free drainage 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 free drainage conditions while it was 99 days under waterlogged conditions. 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 a week.

Although plants under waterlogged conditions had delayed heading and maturity days, they achieved almost equivalent plant height to those of the plants in the free drainage 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. Hence, at the end, 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 plants in the free drainage experiment. There was a marked difference for grain yield, however, and this was expected because waterlogged and free drainage plants had apparent differences in total productive tillers. The difference in grain yield spike^{-1} between the free drainage and waterlogged plants of Feres Gama (37) is 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 which indicates differences in the relative sensitivity of the landraces to waterlogging stress. Moreover, 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 Feres Gama(37) as their parent (Table 1). The reverse is true under free drainage conditions. This indicates differences between landraces and their progenies in the expression of their genetic potential under drained and waterlogged situations.

Table 1 : Performance under waterlogged and free drainage growth conditions of parents and F1 progenies from a pot experiment in a greenhouse

Parents	DHE			DMA			PLH			SPL			NS/SP			GY/SP			GY/Plot		
	WL	FD	D	WL	FD	D	WL	FD	D	WL	FD	D	WL	FD	D	WL	FD	D	WL	FD	D
F.Gama(37)	116a	102a	14	165	152a	13	88	89	-1	6.4b	7.1a	-0.7	22	44a	-22	1.04	2.28a	-1.24	4.03	7.87	-3.84
Feleme(68)	95bc	81b	15	144	138b	6	79	82	-3	6.2b	5.5c	0.7	38	28c	10	1.80	1.39b	0.40	7.05	8.76	-1.72
Mage(07)	91c	77b	14	144	132c	12	79	83	-4	6.1b	5.7c	0.4	32	27c	5	1.69	1.48b	0.21	5.32	7.32	-2.00
1182(44)	97b	75b	22	142	137bc	5	81	82	-1	3.9c	4.2d	-0.3	26	28c	-2	1.13	1.45b	-0.31	4.64	6.29	-1.65
1153(28)	96bc	81b	16	142	132c	10	82	82	0	6.9a	6.3b	0.6	30	37b	-7	1.73	2.00a	-0.27	5.56	9.23	-3.66
$LSD_{0.05}$	5.8	5.6		4.3	5.2		NS	NS		0.5	0.47		NS	6.25		NS	0.29		NS	NS	
C.V (%)	6.2	7.1		3.0	3.9		7.7	6.1		8.6	8.6		35.0	19.9		33.5	17.8		44.1	18.9	
	DHE			DMA			PLH			SPL			NS/SP			GY/SP			GY/Plot		
F1progenies	WL	FD	D	WL	FD	D	WL	FD	D	WL	FD	D	WL	FD	D	WL	FD	D	WL	FD	D
P1 X P2	110	84	26	144	141	3	79	80	-1	7.4	6.6	0.8	34	42	-8	1.58	2.21	-0.63	5.29	9.16	-3.87
P1 X P3	104	87	17	152	141	11	87	84	3	7.0	6.6	0.4	41	44	-3	1.87	2.01	-0.14	7.49	9.29	-1.80
P1 X P4	106	81	25	151	136	15	78	91	-13	7.1	7.1	0.0	27	47	-20	1.54	2.48	-0.94	6.15	10.25	-4.10
P1 X P5	107	88	19	153	142	11	81	89	-8	6.9	7.6	-0.7	29	41	-12	1.65	2.34	-0.69	7.61	10.82	-3.21
P2 X P3	92	81	11	142	137	5	86	81	5	6.6	5.6	1.0	38	33	5	2.02	1.55	0.47	7.87	8.65	-0.78
P2 X P4	94	78	16	142	133	9	78	79	1	6.4	6.2	0.2	37	31	6	1.63	1.64	-0.01	6.31	7.61	-1.30
P2 X P5	99	81	18	139	143	-4	78	83	-5	6.6	6.6	0.0	29	33	-4	1.63	1.65	-0.02	6.49	9.91	-3.42
P3 X P4	101	79	22	143	132	11	92	-	-	7.1	6.5	0.6	40	33	7	2.22	1.64	0.58	7.90	8.55	-0.65
P3 X P5	92	75	17	138	135	3	84	80	4	6.8	6.5	0.3	41	31	10	2.10	1.73	0.37	8.26	8.14	0.12
P4 X P5	93	79	15	139	131	8	81	85	-4	6.4	6.2	0.2	37	43	-6	2.09	1.97	0.12	8.07	10.57	-2.50
$LSD_{0.05}$	6.9	3.8		5.3	5.2		NS	NS		NS	0.46		NS	7.2		NS	0.37		NS	1.52	

DHE=days to heading; DMA = days to maturity; PLH = plant height (cm); NS/SP = number of seeds spike^{-1}; GY/SP = grain yield spike^{-1}; GY/plot = grain yield plot^{-1}; D = difference; P1 to P3 are symbols representing parents listed in order in the table.

b) Combining Ability Effects

Under waterlogging conditions, the analysis of variance showed significant mean square values of general combining ability (GCA) for days to heading, days to maturity, number of seeds spike^{-1} and grain yield spike^{-1}, but not the specific combining ability (Table 2) implying additive genetic mechanisms might be important in determining these characters. Consistent with the free drainage treatment, GCA for days to heading, days to maturity, and grain yield spike^{-1} were significant under conditions of waterlogging. Both GCA and SCA mean square values were highly significant for spike length under both treatment levels, however, suggesting the importance of both additive and dominant gene action 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 free drainage treatment, grain yield appeared to be determined both by additive and dominant gene action as observed from the low GCA/SCA ratio.

Several combining ability studies in barley (Hockett et al., 1993; Bhatnagar & Sharma, 1995; Schittenhelm et al., 1996; Bhatnagar & Sharma, 1997; Hanifi & 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 are important for yield and yield components. A genetic study for tolerance to waterlogging in barley is lacking and a comparison with other studies is not possible. Based on the result from the free drainage experiment, it can be deduced that in absence of significant SCA effects the performance of the crossed progenies could be predicted based on GCA estimates of the parents because the parents with higher GCA estimates would be expected to produce superior cross bred progenies. In this regard Feres Gama(37) and 1153(28) were found to be good combiners. It was reported, however, that crosses between good general combiners would not always result in good F_1 combinations (Wells & Lay, 1970; Shriva stava & Seshu, 1983).

Table 2 : Combining ability analysis of F_1s and parents in a 5 x 5 diallel crosses of barley landrace lines evaluated under freely drained (FD) and waterlogged (WL) conditions in a greenhouse

Source of variation	Expt.	DF	Agronomic characters						
			DHE	DMA	PLH	SPL	NS/SP	GY/SP	GY
GCA	FD		134.511***	92.253***	26.051	1.314***	107.730***	0.361***	1.852*
	WL		153.167***	148.853***	6.854	0.877***	39.421	0.173	1.467
SCA	FD	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	FD	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	FD		13.16	7.270	3.415	3.450	5.280	9.750	1.240
	WL		14.88	13.940	-	1.507	-	2.080	

Expt.=experiment; FD=free drainage; WL=waterlogged; DHE=days to heading & DMA= days to maturity; PLH=plant height; SPL=spike length;

NS/SP=number of seeds Spike^{-1}; GY/SP=grain yield spike^{-1} and GY=grain yield. * and ****= significantly different at P<0.05 and P<0.001, respectively.

Table 3 : General combining ability (GCA) effect of parents and mean performance for agronomic traits of barley landrace lines from evaluation of a diallel cross under free drainage conditions

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	
C.V(%)	7.1		3.9		6.0		8.6		19.9		17.8		18.9	
Gi		1.579		1.709		NS		0.163		2.366		0.122		0.536
Gi-Gj		2.498		2.703		NS		0.258		3.742		0.192		0.847

Table 4 : General combining ability (GCA) effect of parents and mean performance for agronomic traits of barley landrace lines from evaluation of a diallel cross under waterlogged conditions

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	
C.V(%)	6.2		3.0		7.7		8.6		35.0		33.5		44.0	
Gi		2.333		1.748		NS		0.194		NS		NS		NS
Gi-Gj		3.688		2.764		NS		0.307		NS		NS		NS

DHE=days to heading & DMA= days to maturity; PLH=plant height; SPL=spike length; NS/SP=number of seeds spike^{-1}; GY/SP=grain yield spike^{-1} and GY=grain yield. * and **= significantly different at P=0.05 and P=0.01, respectively; NS = none significant.

The patterns of GCA effects of parents for days to heading and days to maturity are similar for the free drainage and waterlogging treatments in that the three early lines, Mage(07), 1182(44), and 1153(28), all had negative GCA effects for days to heading and maturity and Feres Gama(37) had positive GCA effects at both treatments (Tables 8.5 & 8.6). Earliness is a desirable feature and crosses involving these lines are expected to provide on average early heading and maturing progenies regardless of the waterlogging or free drainage treatments. Mage(07) and 1182(44) had negative GCA effects on yield and yield components, however, and 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 it has consistently higher positive GCA effects for yield and yield components than all other parents under waterlogged conditions. The non-significant GCA mean square values for yield and yield components except spike length put the importance of this line in question, however. Under the free drainage environment, among the early lines, 1153(28) had positive GCA effects for all yield components and implicated 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. Moreover, the GCA effects of Feres Gama(37) is higher than GCA effects of the other parent lines in all cases and the effects were significant for all characters observed under free drainage condition (Table 3).

Generally, under free drainage conditions, Feres Gama(37) and 1153(28) contributed the highest positive GCA effects for yield and yield components (spike length, number of seeds spike^{-1} and grain yield spike^{-1}). They 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 crosses. This cross is also among the top in number of seeds spike^{-1} in the free drainage experiment (Table 5). The facts that GCA effects of 1153(28) for number of seeds spike^{-1} and grain yield spike^{-1} were not significant imply, however, that this parent is not as good a combiner as 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.

Although Feres Gama(37) had significant positive GCA effects for days to heading and maturity, under free drainage 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) which had positive SCA effects for days to maturity (Table 5). SCA mean square values were not significant, however, for these characters under both treatment levels. Hence, it is not important to discuss SCA effects. Therefore, restricting the discussion to spike length and grain yield in which both GCA and SCA mean square values were significant in the free drainage experiment (Table 2), high and positive SCA effects with improved 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) in which spike length of these crosses is above the high parent of the respective crosses. Higher SCA effects for grain yield were also observed in these three crosses and 1182(44) x 1153(28) in which grain yield crosses and 1182(44) x 1153(28) in which grain yield was far above the high parent value of the respective parents (Table 5). In this of experimental set, 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 one poor general combiner for these characters. According to Singh et al. (1985) such crosses would be expected to produce desirable transgressive segregants if the additive genetic system present in the good combiners (1153(28) and Feres Gama(37) and complementary epistatic effects present in the F_1 act in the same direction to maximize the desirable attributes. Under waterlogging conditions only spike length appeared to have significant SCA mean squares and the highest positive SCA effects were noted for crosses between Feres Gama(37) x Feleme(38), Mage(07) x 1182(44) and Feres Gama(37) x 1182(44). The highest mean spike lengths, among all F1, were also observed from these crosses.

Table 5 : Mean agronomic performance and specific combining ability effects of F1 progeny from diallel crosses of landrace lines evaluated under free drainage 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) xFeleme(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	
C.V (%)	5.82		4.4		7.8		19.8		19.90		19.40	

DHE & DMA= days to heading and maturity, respectively; SPL= spike length; NS/SP=number of seeds per spike; GY/SP=grain yield per spike
GY=grain yield; *=significantly different at 0.05 probability.

In the free drainage experiment, GCA and SCA variance estimates associated with each parent (Table 6) indicated that Feres Gama(37) and 1153(28) had comparable SCA variances for yield and yield components suggesting that both parents transferred uniformly their potential to improve yield and yield components to their progeny. However, the relatively lower SCA variance for spike length associated with 1153(28) indicated that the potential for improved spike length was transferred better by this parent than Feres

Gama (37). Under waterlogged conditions, neither yield nor yield components had significant GCA and SCA mean square values except spike length which was also the case in ordinary analyses of variance. Hence a comparison of GCA and SCA variances associated with each parent would not be fair and results are not presented. A parent with comparatively lower SCA variance for a particular trait is said to transfer its potential uniformly to all the F_1 progeny (Griffing, 1956b; Boghi & Perenzin, 1994). Hence, these parents, Feres Gama(37) and 1153(28), shall be tested thoroughly in order that maximum use of their superior combining ability can be made in future crossing programs for environments free of waterlogging problem.

Table 6 : Estimates of GCA variance ($\delta_{\hat{g}i}^2$) and SCA variance ($\delta_{\hat{s}i}^2$) of parents for the different agronomic characters from a diallel cross of barley landrace lines evaluated under free drainage conditions in a greenhouse

Parents	Variance	DHE	DMA	PLH	SPL	NS/SP	GY/SP	GY
F.Gama(37)	$\delta_{\hat{g}i}^2$	56.788	33.543	6.557	0.36	37.284	0.115	-0.081
	$\delta_{\hat{s}i}^2$	11.276	5.955	7.525	0.186	13.123	0.026	0.871
Feleme(68)	$\delta_{\hat{g}i}^2$	-0.706	-0.746	3.069	0.047	6.341	0.026	-0.174
	$\delta_{\hat{s}i}^2$	4.487	17.596	4.194	0.144	-2.690	-0.013	-0.055
Mage(07)	$\delta_{\hat{g}i}^2$	3.107	5.135	-1.501	0.007	6.119	0.023	0.068
	$\delta_{\hat{s}i}^2$	5.152	-0.871	-1.562	0.234	2.035	-0.018	0.281
1182(44)	$\delta_{\hat{g}i}^2$	10.288	3.883	- 2.038	0.201	-2.444	-0.003	0.085
	$\delta_{\hat{s}i}^2$	-3.703	5.646	4.117	0.484	18.139	0.024	1.557
1153(28)	$\delta_{\hat{g}i}^2$	-0.193	2.027	-2.138	0.047	-2.751	0.000	0.288
	$\delta_{\hat{s}i}^2$	2.136	14.547	0.066	0.062	12.187	-0.012	0.989

$\delta_{\hat{g}i}^2$, $\delta_{\hat{s}i}^2$= general combining ability and specific combining ability variance of each parent, respectively

c) *Estimates of genetic parameters*

Genetic parameters of agronomic characters were estimated from F_1 progenies and parents evaluated under free drainage and waterlogging stress. Estimates of the parameters from the respective experiments are presented in Table 7 and 8. The results from the free drainage experiment elucidated that of the total genotypic variance ($\delta^2 g = \delta^2_A + \delta^2_D$), the additive genetic variance portion is very high for all characters except for grain yield in which the δ^2_D is greater than the δ^2_A and spike length that showed comparable values of δ^2_A and δ^2_D. Spike length was the only character that displayed significant SCA mean squares hence relatively higher δ^2_D. However, the additive genetic variance was lower than the dominance variance (δ^2_D) under waterlogged conditions. 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. Dabholkar (1992), however, indicated that it is erroneous 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 & Mackay, 1996). Hence in view of this, it may be assumed that spike length is not under the control of 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.

The predominant role of non-additive gene action in the inheritance of grain yield (Kudla & Kudla, 1995; Bouzerzour, & Djakoune, 1997), the importance of additive gene action in determining grain yield spike^{-1} and heading date (Kudla & Kudla, 1995; Esparza-Martinez & Foster, 1998), and number of seeds spike^{-1} (Bouzerzour, & Djakoune, 1997) has been reported in environments free of stress. In this study, although grain yield appeared to be governed both by additive and non-additive gene actions under free drainage conditions, yield components were found to be under the effects of additive gene action that is in harmony with most of the above studies. By contrast, the importance of both additive and non-additive gene actions for yield and yield components (Bhatnagar & Sharma, 1995; Phogat et al., 1995a) and for days to heading and maturity (Singh & Singh, 1990a) have been reported which is in contrast to this experiment under free drainage conditions. Under waterlogging stress, the additive genetic variance (δ^2_A) for days to heading and days to maturity were very high in contrast to their respective dominance variance (Table 8) indicating the importance of additive gene actions in the expression of these characters which was consistent with the results from the free drainage experiment.

Table 7 : Estimates of genetic parameters for seven agronomic characters of F1s from a diallel cross of barley landrace lines evaluated under free drainage 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	134.511	10.219	5.684	18.404	4.535	36.807	4.535	41.343	47.026	0.88	0.78	0.89
DMA	92.253	12.680	6.656	12.228	6.024	24.456	6.024	30.480	37.136	0.82	0.66	0.80
PLH	26.051	7.628	8.203	2.549	-0.575	5.099	-0.575	4.524	12.727	0.35	0.40	1.13
SPL	1.314	0.381	0.061	0.179	0.320	0.358	0.320	0.678	0.739	0.92	0.48	0.53
NS/SP	107.730	20.401	12.758	13.567	7.643	27.134	7.643	34.777	47.535	0.73	0.57	0.78
GY/SP	0.361	0.037	0.034	0.047	0.003	0.093	0.003	0.096	0.130	0.71	0.72	0.97
GY	1.852	1.497	0.654	0.171	0.843	0.342	0.843	1.185	1.839	0.64	0.19	0.29

Table 8 : Estimates of genetic parameters for the different agronomic characters of F1s and parents from a diallel cross of barley landrace lines evaluated under situations of waterlogging for three weeks in a greenhouse pot experiment

Variable	MSgca	MSsca	δ^2e	δ^2gca	δ^2sca	δ^2_A	δ^2_D	δ^2g	δ^2p	h^2b	h^2n	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	-

*, *** = significantly different at P < 0.05 and P < 0.001, respectively. – represents GCA:SSA ratio not calculated because neither GCA nor SCA mean square values were significant

Estimates of broad sense heritability (*h^2b*) were in the range of 0.35 for plant height to 0.92 for spike length under free drainage condition and 0.00 for grain yield to 1.03 for grain yield spike^{-1} under waterlogged conditions. Values for narrow sense heritability (*h^2n*) were in the range of 0.19 for grain yield to 0.78 for days to heading in the free drainage experiment while it was 0.00 for grain yield to 0.79 for days to heading in the case of waterlogging experiment. Heritabilities for the reproductive characters (number of seeds spike^{-1}, grain yield spike^{-1} and grain yield) were very low to moderate in the free drainage experiment whereas both *h^2b* and *h^2n* were moderate to very high for the phonological characters for both treatment levels. Higher heritability estimates reported for days to heading (Frey, 1954; Singh & Singh, 1990a; Cai et al., 1993), and number of estimates reported for days to heading (Frey, 1954; Singh & Singh, 1990a; Cai et al., 1993), and number of seeds spike^{-1} (El-Hennawy, 1997) and low heritability for grain yield (Grafius et al., 1952; Cai et al., 1993; Bailey & Wolfe, 1994; Phogat, et al., 1995) in barley are in agreement with results obtained from the free drainage experiment.

It is obvious that heritability in the broad sense may be regarded as an estimate of the upper bound of heritability in the narrow sense since it includes both the additive and non-additive genetic variances. Hence, it should not be preferred if h^2n is available because it is the h^2n which expresses the extent to which the phenotypes are determined by the genes transmitted from the parents (Bos & Caligari, 1995). Moreover, heritability in the narrow sense being the ratio of the additive genetic variance to the phenotypic variance is a scale-independent quantity and plays an important role in predicting the response to selection. In view of this, the very low additive variance compared to the dominance variance and the consequently very low h^2n for grain yield in the free drainage experiment (Table 7) imply that genetic advance by selecting for this character is expected to be low. On the other hand, because of the absence of the dominant genetic variance for grain yield per spike, higher h^2n was observed. Hence, it is possible to select barley plants with a desirable grain yield per spike in early generations, and indirect selection for grain yield through selection for grain yield per spike appears to be feasible under free drainage environment. It's predictability (PR=0.97) was also higher compared to all other yield components.

The waterlogged experiment was generally characterized by negative estimates of genetic parameters that were not the case with data from the free drainage experiment. Miller et al. (1958) discussed negative estimates of genetic parameters and attributed it to sampling error and the negative estimates shall be regarded as zero values. 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 & 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 & 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 9 : Comparisons of mean performance of F1 progenies under free drainage condition and statistical significance for the difference between the progenies and their respective mid-parent values

Crosses	DHE			DMA			SPL			NS/SP			GY/SP			GY/pot		
	F1	MP	t-test	F1	MP	t-test	F1	MP	t-test	F1	MP	t-test	F1	MP	t-test	F1	MP	t-test
P1 x P2[a]	84	91	**	141	145	NS	6.6	6.3	NS	42	36	NS	2.21	1.83	NS	9.15	8.34	NS
P1 x P3	87	90	NS	141	142	NS	6.7	6.4	NS	44	36	NS	2.01	1.88	NS	9.30	7.59	NS
P1 x P4	81	89	**	136	144	*	7.1	5.7	**	47	36	*	2.48	1.86	**	10.25	7.08	**
P1 x P5	88	91	NS	142	141	NS	7.6	6.7	**	41	41	NS	2.35	2.14	NS	10.82	8.55	*
P2 x P3	81	79	NS	137	135	NS	5.6	5.6	NS	33	28	NS	1.55	1.43	NS	8.65	8.04	NS
P2 x P4	78	78	NS	133	137	NS	6.2	4.9	***	31	28	NS	1.64	1.42	NS	7.61	7.53	NS

P2 x P5	81	81	NS	143	135	*	6.6	5.9	*	33	33	NS	1.65	1.69	NS	9.91	8.99	NS
P3 x P4	79	76	NS	132	134	NS	6.5	4.9	***	33	28	NS	1.64	1.46	NS	8.55	6.80	NS
P3 x P5	75	79	NS	130	132	NS	6.5	6.0	NS	31	32	NS	1.73	1.72	NS	8.14	8.27	NS
P4 x P5	79	78	NS	132	134	NS	6.2	5.3	**	43	33	*	1.97	2.00	NS	10.57	7.76	**

Table 10 : Comparisons of mean performances of F1 progenies under waterlogged condition and statistical significance of the differences between the progenies and their respective mid-parent values

Crosses	DHE			DMA			SPL			NS/SP			GY/SP			GY/pot		
	F1	MP	t-test	F1	MP	t-test	F1	MP	t-test	F1	MP	t-test	F1	MP	t-test	F1	MP	t-test
P1 x P2[a]	110	106	NS	144	155	***	7.4	6.3	***	34	30	NS	1.58	1.42	NS	5.29	5.54	NS
P1 x P3	104	104	NS	152	155	NS	7.0	6.2	*	41	27	*	1.87	1.36	NS	7.49	4.67	NS
P1 x P4	106	107	NS	151	154	NS	7.1	5.1	***	27	24	NS	1.54	1.08	NS	6.15	5.33	NS
P1 x P5	107	106	NS	153	155	NS	6.9	6.6	NS	29	26	NS	1.65	1.38	NS	7.61	4.79	NS
P2 x P3	92	93	NS	142	144	NS	6.6	6.1	NS	38	35	NS	2.02	1.74	NS	7.87	6.18	NS
P2 x P4	94	96	NS	142	143	NS	6.4	5.1	***	37	32	NS	1.63	1.46	NS	6.31	5.84	NS
P2 x P5	99	96	NS	139	144	NS	6.6	6.5	NS	29	34	NS	1.63	1.76	NS	6.49	6.30	NS
P3 x P4	101	94	NS	143	143	NS	7.1	5.0	**	40	29	NS	2.22	1.41	*	7.90	4.98	NS
P3 x P5	92	94	NS	138	145		6.8	6.5	NS		31	NS	2.10		NS	8.26	5.44	NS
P4 x P5	93	97	NS	139	144	NS	6.4	5.4	**	37	28	NS	2.09	1.43	NS	8.07	5.10	NS

P1=Feres Gama(37), P2=Feleme(68), P3=Mage-07, P4=1184(44), & P5=1153(28); *, **, & *** indicate significantly different values at 0.05, 0.01 & 0.001 probability levels, respectively. MP=Mid-parent value

V. Conclusions

The fact that there are two contrasting barley production environments in north Shewa (areas prone to waterlogging and areas free of waterlogging stress) and because there is evidence that genetic variances, genetic correlations between characters and effectiveness of selection differ in stress and non stress environments prompted the evaluation of the F1 progenies under conditions of free drainage and waterlogging stress. The results elucidated the importance of general combining ability (GCA) for days to heading and days to maturity at both treatment levels and for number of seeds spike^{-1} and grain yield spike^{-1} in the free drainage experiment only indicating the significance of additive gene effects for these characters. In free drainage conditions, grain yield appeared to be determined both by additive and dominant gene actions, however. Both GCA and SCA were significant for spike length at both treatment levels but the higher GCA:SCA ratio and the higher GCA variance (δ^2gca) in the free drainage experiment indicated that this character is also under the control of additive gene action. By contrast, although GCA:SCA ratio was higher for this character in the waterlogging experiment, SCA variance (δ^2sca) was greater than the δ^2gca. Hence, spike length is not under the control of additive gene action under waterlogging stress.

The patterns of GCA effects of parents for days to heading and days to maturity are similar for both treatment levels but different for the other characters. Among the parents, the two late and early maturing lines, Feres Gama(37) and 1153(28), respectively contributed the highest positive GCA effects for yield and yield components in the free drainage experiment. Accordingly, the cross between these two parents gave the highest mean spike length, grain yield spike^{-1} and grain yield than all crosses and is among the top in number of seeds spike^{-1}. The fact that GCA effects of 1153(28) for number of seeds spike^{-1} and grain yield spike^{-1} were not significant imply that this parent is not as good a combiner as Feres Gama(37) for these characters, but it is as good as Feres Gama(37) in its combining ability for spike length. Moreover, the difference for GCA effects of the two parents for spike length is significant denoting that both parents are equally desirable. In conditions of waterlogging, Mage(07) had consistently higher positive GCA effects for yield and yield components than all other parents. The non significant GCA mean square values for yield and yield components except spike length under waterlogged conditions put the importance of this line in question, however.

GCA and SCA variance estimates associated with each parent also indicated that Feres Gama(37) and 1153(28) had comparable SCA variances for yield and yield components in the free drainage experiment suggesting that both parents transferred their genetic potential for yield and yield components effectively to their progeny. However, the relatively lower SCA variance for spike length associated with 1153(28) indicated that this parent transferred its genetic potential to its progeny better than Feres Gama(37). Under waterlogged conditions, neither yield nor yield components had significant GCA and SCA mean square values except spike length which was also the case in ordinary analyses of variance. Hence a comparison of GCA and SCA variances associated with each parent would not be fair. The negative estimates of genetic parameters observed for most characters under waterlogged conditions except for days to heading and maturity imply the difficulty in achieving the anticipated progress through selection for quantitative characters. By the same token, the non significant GCA effects of parents under waterlogged conditions also illustrated the difficulty in predicting the performance of progenies under waterlogged conditions.

It can be generalized that Feres Gama(37) and 1153(28) were found to be good combiners and they shall be tested thoroughly in order that maximum use of their superior combining ability can be made in future crossing program aimed at improving yield and yield components for environments free of waterlogging problems. Grain yield spike^{-1} is highly heritable and predictable under free drainage conditions so that good progress can be expected from effective selection for this character. By contrast, the very low heritability (0.19) for grain yield implies that it is very difficult to make progress by selection for grain yield *per se*. Therefore, grain yield spike^{-1} can serve as indirect selection for genotypes with high grain yield since it has highly significant positive genotypic and phenotypic correlation with grain yield also. An important point to note is that the estimates of genetic variances and heritability values were from one experiment in one year. Therefore, the values are likely to be biased upward due to confounding effects of genotype x location, genotype x year and genotype x location x year interaction components. Nevertheless the estimates provide an indication of the relative ease of making progress through breeding.

References Références Referencias

1. Bailey, K.L. and R.I. Wolfe. 1994. Genetic relationship between reaction to common root rot and yield in a progeny of barley cross. *Canadian Journal of plant Pathology* 16(3): 163-169.
2. Baker, R.J. 1978. Issues in diallel analysis. *Crop Sci.* 18:533-536.
3. Bhatnagar, V.K. and S.N. Sharma. 1995. Diallel analysis for combining ability for grain yield and its components in barley. *Indian Journal of Genetics and Plant Breeding* 55(3): 228-232.
4. Bhatnagar, V.K. and S.N. Sharma. 1995. Diallel analysis for combining ability for grain yield and its components in barley. *Indian journal of Genetics and plant Breeding* 55(3): 228-232.
5. Bhatnagar, V.K. and S.N. Sharma. 1997. Diallel analysis for grain yield and harvest index in barley under diverse environments. *Rachis* 16(1-2) publ. 1998: 22-27.
6. Bos, I. and P. Caligari. 1995. Selection methods in plant breeding. Chapman and Hall, London.
7. Bouzerzour, H. and M. Djakoune. 1997. Heritabilities, gains from selection and genetic correlations for grain yield of barley grown in two contrasting environments. *Field Crops research* 41(3):173-178.
8. Cai, Y.H., M.Tahir, and S.K. Yau. 1993. Relationship of growth vigor, leaf color and other agronomic characters with grain yield in winter and facultative barley in low rainfall environment. *Rachis* 12(1-2): 20-23.
9. Ceccarelli, S. 1994. Specific adaptation and breeding for marginal conditions. *Euphytica* 77: 205-219.
10. Ceccarelli, S. 1996. Positive interpretation of genotype by environment interactions in relation to sustainability and biodiversity. In: Cooper, M. and Hammers, G.L. (eds.). Plant Adaptation and crop improvement. CAB International, Wallingford, UK; ICRISAT, Andra Pradesh, India; IRRI, Manila, Philippines. pp. 467-486.

11. Ceccarelli, S. and S. Grando. 1996. Importance of specific adaptation in breeding for marginal conditions. In: Hailu G. and Joop van Leur eds.). Barley Research in Ethiopia: past work and future prospects. Proceedings of the first barley research review workshop, 16-19 Oct., 1993. Addis Ababa Ethiopia. pp 34-58.
12. Ceccarelli, S. S. Grando and J. Hablin. 1992. Relationship between barley grain yield measured in
13. Comstock, R.E. and R.H. Moll. 1963. Genotype-environment interaction. In: Hanson, W.D. and Robinson, H.F. (eds.). Statistical Genetics and Plant Breeding. National Academy of Sciences-National Research Council, Washington DC. pp. 165-196.
14. Dabholkar, A.R. 1992. Elements of Biometrical Genetics. Concept Publication company, New Delhi.
15. Dudley, J.W., and R.H. Moll. 1969. Interpretation and use of estimates of heritability and genetic variances in plant breeding. Crop Sci.9: 257-262.
16. Esparza-Martinez, J.H. and A.E. Foster. 1998. Genetic analysis of days to flowering and other characteristics of two-rowed barley. *Agricultura Technicaen-Mexico* 24(2): 131-144.
17. Falconer, D.S. 1981. Introduction to quantitative genetics (Second edition). Longman, London.
18. Falconer, D.S. and T.F.C. Mackay. 1996. Introduction to quantitative genetics (fourth edition). Pearson Education Limited. Edinburgh Gate, Harlow. England.
19. Fehr, W.R. 1987. Principles of cultivar development (Vol. 1). Theory and technique. Macmillan Publishing Company, New York. /
20. Frey, K.J. 1954. Inheritance and heritability of heading date in barley. *Agron. J.* 54: 226-228.
21. Gouis J.L.E., D. Beghin, E. Heumez and P. Pluchard. 2002. Diallel analysis of winter wheat at two nitrogen levels. *Crop Sci.* 42: 1129-1134.
22. Grafius, J. E., W.L. Nelson and V.A. Dirks. 1952. The heritability of yield in abrley as measured by early generation bulked progenies. *Agron. J.* 44:253-257.
23. Griffing, B. 1956b. Concept of general and specific combining ability in relation to diallel crossing systems. *Aust. J. Biol. Sci.* 9: 463-493.
24. Haddad, N.I., T.P. Bogyo and F.J. Muehlbauer.1982. Genetic variance of six agronomic characters in three lentil (Lens culinaris Medic) crosses. *Euphytica* 31: 113-121.
25. Hanifi, M.L and A. Gallais. 1999. Heterosis, genetic effects and value of F2s and doubled-haploid lines in barley breeding. *Agronomie* 19(6): 509-520.
26. Hockett, E.A., A.F. Cook, M.A. Khan, J.M. Martin and B.L. Jones. 1993. Hybrid performance and combining ability for yield and malt quality in a diallel cross of barley. *Crop Sci.* 33(6): 1239-1244.
27. Hogarth, D.M.1971. Quantitative inheritance studies in sugarcane I. Estimation of variance components. *Aust. J. Agric*. Res. 22:93-102.
28. Kudla, M.M. and M. Kudla. 1995. Genetic possibilities of increasing yield in spring barley. *Biuletyn instytutu Hodoli Aklimatyzacji Rosin* 193: 35-44.
29. Lakew B., Y. Semeane, F. Alemayehu, H. Gebre, S. Grando, J.A.G van Leur and S. Ceccarelli.1997. Exploiting the diversity of barley landraces in Ethiopia. *Genetic Resources and Crop Evolution 44: 109-116.*
30. Maluf, W.R., J.E.C. Miranda and P.E. Ferriera.1983. Broad sense heritabilities for root and vine traits in sweet potatoes (Ipomoea batatus (L.). LAM). *Brazil J. Genetics* VI (3): 443-451.
31. Matzinger, D.F. 1963. Experimental estimates of genetic parameters and their applications in self-fertilizing plants. In: Hanson, W.D. and Robinson, H.F. (eds.). Statistical genetics and plant breeding. National Academy of Sciences-National research Council. Washington D.C. pp.253-279.
32. Mayo, O. 1987. The theory of plant breeding (second edition). Oxford Science Publications.
33. Muehlbauer F.J., W.J. Kaiser, S.L. Clement and R.J. Summerfield.1995. Production and breeding of lentil. *Advances in Agronomy* 54: 283-332.
34. Phogat, D.S., D. Singh, G.S. Dahiya and D. Singh. 1995a. Genetics of protein content and yield in barley (*Hordeum vulgare* L.) *Crop Research-Hisar* 9(1): 85-92.
35. Phogat, D.S., D. Singh, G.S. Dahiya and D. Singh. 1995b. Genetics of yield and yield components in barley (Hordeum vulgare L.). *Crop Research-Hisar*, 9(3): 363-369.
36. Roy, N.M. and B.R. Murty. 1970. A selection procedure in wheat for stress environments. *Euphytica* 19: 509-521.
37. Schittenhelm, S.J., A. Okeno and W. Friedt. 1996. Prospects of agronomic improvement in spring barley based on comparison old and new germplasm. *Journal of Agronomy and Crop Science* 176(5): 295-303.
38. Shibin, C., C. Yang, F. Xianwen, S.B. Cai, Y. Cao, and X.W. Fang. 1996. Studies on the variability and combining ability of waterlogging tolerance of common wheat. *Jiangsu Journal of Agricultural Sciences* 12 (3): 1-5.
39. Shrivastava, M.N. and D.V. Seshu. 1983. Combining ability for yield and associated characters in rice. *Crop Sci.* 23:741-744.
40. Singh, M., S. Ceccarelli and J.Hamblin. 1993. Estimates of heritability from varietal trials data. *Theor. Appl. Genet.* 86:437-441.
41. Singh, S.J. and B.D.Singh. 1990a. Genetics of earliness in barley. *Crop Improvement* 17(2): 172-174.
42. Sprague, G.F. 1966. Quantitative genetics in plant improvement. In: Frey, K.J. (ed.). Plant breeding.

The Iowa State University Press. Ames, Iowa. pp.315-354.

43. Wells, D.G and C.L. Lay. 1970. Hybrid vigor in red spring wheat crosses. *Crop Sci*. 10: 220-223.
44. Witcombe, J.R. and D.S. Virk, 2001. Number of crosses and population size for participatory and classical plant breeding. *Euphytica* 122: 451-462.