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EVALUATION OF GENERAL AND SPECIFIC COMBINING ABILITY FROM A FOUR GENERATION WHEAT DIALLEL*

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Abstract

The F_1, F_2, backcross and selfed backcross generations of a five parent complete diallel cross of common wheat (*Triticum aestivum* L.) were used as materials in the study. The experimental data for two locations were analysed with respect to general and specific combining ability. The inter-location effects were assessed by factorial ANOVA and stability of five cultivars over two locations was evaluated through regression analysis. The characters considered were: Onset-of-heading. Final heading. Heading-span, Plant height, Number of tillers per plant, Number of spikelets per spike. Number of seeds per spike, Weight of seeds per spike, 1000-kernel weight and Yield of grains per plant.

The general and specific combining ability analyses indicated that the parental lines possessing high GCA's usually produced hybrids with low SCA's and therefore general combining ability of the parents does not necessarily constitute a criterion for evolving hybrirds with high specific combining ability. The variances of GCA's were usually greater than those of SCA's for all the characters, and in cases where SCA variances were larger, the importance of non-additive gene effects for the characters concerned has been emphasized. SCA variances significantly higher than GCA variances indicated instability of the cultivar for the particular character and therefore these differences may be used as criteria for selection in pedigree-record breeding. The mean squares for GCA's were in general all significant. The analysis also showed that the GCA's were not significantly affected either by diallel generations or by locations. The stability response for each cultivar with respect to its GCA was consistent over two locations.

Introduction

The ultimate object of a plant breeding programme is to evolve superior yielding cultivar with higher heritability and wider adaptability. This greatly depends upon the knowledge of combining ability of the parental lines used in the project under study. Combining ability *per se* may be defined as the ability of the two parents to transmit favourable or unfavourable characters to their progeny. In biometrical genetics, two types of combining abilities are considered, viz., general combining ability (GCA), refering to the average performance of a parental line as reflected in its hybrid combinations and, specific combining ability (SCA), as an average performance of a particular cross. According to Sprague and Tatum (1942), general combining ability is due to the genes which are largely additive, and specific combining ability to genes showing non-additive effects. Fryxell *et al* (1958) consider general combining ability as the ability of a parental strain to produce promising or non-promising genotypes in its hybrids regardless of the other parent involved, while specific combining ability refers to this ability in hybrid combinations with certain other parental strains.

The importance of combining ability studies lies in the assessment of the parental lines and their hybrids respectively showing significant additive and non-

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additive gene effects with respect to a particular character. This also serves as a criterion in screening the desirable entries on the basis of their general and specific combining ability values. This becomes even more informative and effective if the combining abilities are tested for more than two years and at more than two locations because, the analysis of genotype-environmental interaction with respect to general and specific combining ability, replicated in time, and space or in both, will provide information on the pattern of reaction of homozygous parents and their hybrids to environmental variation.

The measurement of genotype-environmental interaction in the diallel cross provides an assessment of a number of parental strains together with their hybrid combinations. The project reported in this paper deals with this type of analysis of genotype-environmental interaction in a five parent diallel cross of common wheat (*Triticum aestivum* L. em Thell). The purpose of the investigation was to obtain information regarding the extent to which the general and specific combining abilities of the parents and their hybrids, tested over four generations of diallel and replicated at two locations, are affected by environmental changes

Material and Methods

The experimental material consisted of a five-cultivar, four-generation complete diallel cross accomplished during 1970-72 and grown over two locations in Canada, viz., Department of Genetics Ellerslie Field Lab and the Department of Plant Science Parkland Farm of the University of Alberta, Edmonton, in 1972. The parental lines, Marquis, Chinook (both Canadian), Khush-hal (Pakistani), Ciano and Inia (both Mexican) were selected on the basis of their diversity of origin, different spike and seed characteristics, early and late maturity periods and the yield performances. The diallel generations considered were F_1's, F_2's, backcrosses (B_0's) and selfed backcrosses (B_1's). The whole of the experimental material was space seeded, at each of the location, in an incomplete block design of 15×15 partially balanced triple lattice type. The other experimental details are discussed by Soomro (1974, 1975) and Soomro & Aksel (1975). Following observations were recorded at each of the location:

1. Onset-of-heading: Expressed as the number of days between the date of seeding and the appearance of the first head in the row or entry.
2. Final-heading: Recorded in number of days from the date of seeding to the day when 75% of the plants had headed in that row.
3. Heading-span: Measured by the difference between (1) and (2).
4. Plant height: Measured in centimeters from the surface of the soil to the tip of the spike on the highest tiller, excluding awns. Ten consecutive plants per row were recorded for height irrespective of their growth performance leaving the first plant as border effects except in the rows where the number of surviving plants were reduced to ten or less. At maturity only those plants were harvested that had been recorded for height. Following observations on yield and yield components were recorded on the harvested material.

5. Number of productive tillers per plant.

6. Number of spikelets per spike: Three spikes were taken at random from each plant and their spikelets counted.

7. Number of seeds per spike.

8. Weight of seeds per spike: Spikes randomly sampled for spikelets-count were threshed separately and their seeds counted and weighed.

9. 1000-kernel weight in grams: Computed from observations (7) and (8).

10. Yield of grains per plant in grams: Expressed as total seed weight of all the spikes including those used for (6), (7) and (8).

Statistical analysis:

The means were calculated for all the characters except onset-of-heading, final heading and heading-span. For observations (6), (7) and (8), means of three readings were calculated first and then treated as individual variables for the calculation of entry means. These were categorized into four diallel tables, viz., F_1's, F_2's, backcrosses and selfed backcrosses. General and specific combining ability analyses, for each of the diallel tables and for each of the character, were performed following Griffing's (1956) method 1 (where all the n^2 entries of the diallel table are included), model 1 (where the experimental material is not regarded as a random sample from the population). Model 1 was chosen against model 2 (where the experimental material is regarded as a random sample from the population) because the parental lines, producing all the entries in the form of various combinations, were deliberately chosen for the present study. The following mathematical model for combining ability analyses was used:

$$x_{ij} = \mu + g_i + g_j + S_{ij} + r_{ij} + \frac{1}{bc} \sum_{k}^{b} \sum_{l}^{c} e_{ijkl}$$

where, x_{ij} is the mean performance of ijth genotype, μ is the population mean, g_i and g are the GCA effects of ith and jth parents, s_{ij} is the SCA effect for the cross between ith and jth parent such that $s_{ij} - s_{ji}$ and r_{ij} is the reciprocal effect involving the cross between ith and jth parent (including reciprocal) such that $r_{ij} - r_{ji}$. The e_{ijkl} is the environmental effect associated with $i_{jkl}th$ individual observation. In this model, subscripts i, j are the parents from 1 to n, k are the blocks from 1 to b, and l are the total number of observations (entry means) from 1 to c. The various effects thus estimated are given hereunder (Griffing, 1956):

$\mu = 1/n^2 X..$

$g_i = 1/2n\ (Xi. + X.i) - 1/n^2 x..$

$s_{ij} = \frac{1}{2}(x_{ij} + x_{ij}) - 1/2p\ (X_i. + X.i + X_j. + X.j) + 1/n^2 X..$

$r_{ij} = \frac{1}{2}(x_{ij} - x_{ij})$

Where: n = number of the parents used in the diallel table

X.. = sum of all the entry-means of the diallel table

Xi. = sum of those crosses in which ith parent is used as ♀ parent

X.i = sum of those crosses in which ith parent is used as ♂ parent

Xj. = sum of the crosses in which jth parent is used as ♀ parent

X.j = sum of the crosses in which jth parent is used as ♂ parent

xij and xji = mean performance of ijth and jith genotype.

In case of F_2 generation, where the hybrids were duplicated in each replication at both locations (Soomro 1974), though the heading data and yield observations were recorded separately for the two repititions, the analysis of general and specific combining ability is based on their average. The backcross and selfed backcross diallel tables were considered equivalent to those of the F_2 and F_3 diallel matrices (analogous to Jinks 1956) by amalgamating four backcross entries to compute the corresponding off- diagonal cell of the analoged matrix (Soomro 1974). The general and specific combining ability estimates were then based on these so called normalized backcross and selfed backcross diallel tables.

Experimental Results

The general combining ability values of the five-parental lines in case of F_1, F_2, backcross and selfed-backcross diallel tables may be viewed from Tables 1 to 10. Marquis scored highest in GCA for onset-of heading (Table 1) at both locations for all the diallel sets except in F_1 diallel at Parkland, where Chinook excelled Marquis. Ciano ranked lowest in GCA for onset-of-heading at both locations and for all the diallel sets. For final heading (Table 2), Marquis at Ellerslie and Chinook at Parkland ranked highest for all the diallel generations while Ciano was the lowest except for backcross diallel set at Ellerslie where Inia scored lowest. Chinook scored highest GCA for heading-span (Table 3) in all the diallel sets at both locations except for backcross diallel at Ellerslie where Marquis was the highest while Inia was the lowest except in F_1 diallel at Ellerslie and selfed backcross diallel at both locations where Ciano excelled Inia. The highest general combining ability of Marquis or Chinook for heading data implies that the particular parental lines, though best combiners, require more number of days to head and therefore are assumed to be late-maturing. This is considered to be the undesirable character in plant breeding programmes and therefore the entries with lowest general combining abilities (Ciano and Inia in this case) are preferred as they are early-headers and eventually early-maturing.

In case of plant height (Table 4), Marquis ranked highest in GCA for all the diallel sets at both locations except in F_1 diallel at Parkland where Chinook excelled Marquis while Inia was the lowest in GCA except for F_2 diallel at Parkland where Ciano was the lowest. The highest GCA for plant height categorizes Marquis and Chinook to be the tallest entries while Ciano and Inia possessing lowest GCA's may be considered as short statured cultivars. High GCA for plant height in case of Marquis and Chinook is also not desired as the taller varieties are usually succeptible to lodging and therefore less yielding. If selection is made on height basis, entries with lowest GCA's (Ciano and Inia) have to be given priority.

For number of tillers per plant (Table 5), Chinook at Ellerslie and Khush-hal at Parkland scored high GCA in F_1 diallel set while Inia was the last. In F_2 diallel table, Khush-hal at Ellerslie and Chinook at Parkland ranked highest while Inia was the lowest at both locations. Chinook at Ellerslie and Marquis at Parkland in case of backcross diallel set and Chinook at both locations in selfed backcross diallel set, respectively secured highest GCA's while Inia was the lowest for both the locations. General combining abilities for other yield components, viz., number of spikelete per spike (Table 6), number of seeds per spike (Table 7), weight of seeds per spike (Table 8) and 1000-kernel weight (Table 9) may be interpreted in the similar fashion. As far as yield per plant is concerned (Table 10), Inia possessed highest GCA at both locations in case of F_1 diallel set while Chinook was the lowest. Inia at Ellerslie and Khush-hal at Parkland were the highest in F_2 diallel set while Chinook at Ellerslie and

Marquis at Parkland ranked lowest. Inia had highest GCA in backcross diallel set at both locations while Chinook at Ellerslie and Marquis at Parkland were the lowest. In selfed backcross diallel set, Inia at Ellerslie and Marquis at Parkland ranked first while Chinook at Ellerslie and Ciano at Parkland ranked last.

The estimates of specific combining abilities, for all the characters and for each of the diallel generation at both locations, together with reciprocal effects and variances for general and specific combining abilities are presented in Table 1 to 10. Following conclusions, in general, may be drawn from these results:

(1) The highest SCA value of a hybrid combination for a particular character in a particular diallel table reflects the performance of that entry. Characterwise interpretations may therefore be made accordingly keeping in mind the preference for high (yield and yield components) or low (in cases of heading-data and plant height) SCA scores.

(2) In almost all the cases, the hybrids with high specific combining abilities are associated with one or both of their respective parents of low general combining abilities and *vice versa.* Thus it seems unlikely that the best performing parents (those with high GCA's) necessarily produce hydrids with high SCA's.

(3) Generally the variances of GCA's were larger than those for SCA's and since GCA is the result of additive, and SCA, non-additive gene effects (Sprague & Tatum 1942; Griffing 1956; and Fryxell *et al* 1958), the selection of the parental lines on the basis of their GCA's should be given priority over selection on the basis of their SCA's. This conclusion may also be supported from the analysis of variance for general and specific combining ability (Table 11). The results of this table indicate that the variances for GCA were significant except for heading-span and yield per plant in F_1 and F2 diallel sets and for yield per plant in backcross and selfed backcross diallel generations. The significant variances for SCA imply that the non-additive gene effects for particular characters are relatively more important and that the hybrids with highest SCA's may be selected for further breeding adaptability tests.

(4) The significance of reciprocal effects may be attributed to the female parent of the cross if a positive sign is appended to the effect and to the male parent if the effect has a negative sign. In both the cases the significant reciprocal effects does not necessarily imply significant differences in SCA values of a cross and its reciprocal.

In order to assess the stability of five cultivars with respect to their GCA's, factorial analysis of variance on weighted values of general combining abilities over four generations and two locations was carried out using fixed-effect-model as described by Scheffe (1959). Individual GCA's were standardized by dividing each value of a particular character by the GCA averaged over four generations and two locations, for that character. The aim of such standardization preceding factorial ANOVA was to normalize the scales for different characters. For example, heading were taken in number of days, plant height was measured in centimeters, yield per plant, weight of seeds per spike and 1000-kernel weight were expressed in grams and number of tillers per plant, number of spikelets per spike and number of seeds per spike data were scored as simple counts. Thus by dividing the GCA of each character by its mean over two locations not only the scale differences were removed but the inter-location differences were preserved also.

Table 1. Estimates of GCA, SCA and RE values and of their variances for the character *onset of heading*

Generation: F1

♀ Parent		Specific combining ability (SCA)					GCA	Variance of GCA	Variance of SCA
		Marquis	Chinook	Khush-hal	Ciano	Inia			
Marquis		—	0.8667 — 0.5333		—1.1000	—1.2999	1.9333	3.6535	—0.2104
			0.6801	—0.0866	—0.8866	—1.2533	1.9867	3.7430	—0.5095
Chinook	Reciprocal effects	—0.3333	—	—0.9000	—0.4667	—0.5000	1.4667	2.0669	0.0400
		0.1667		0.3800	0.2467	—1.1200	2.3533	5.3343	—0.3554
Khush-hal		0.0	—0.5000	—	0.1333	0.4333	—0.4666	0.1336	0.1544
		—0.1667	0.0		—0.6867	—0.8867	—0.8800	0.5705	—0.4589
Ciano		—0.5000	0.0	0.6667	—	1.0334	—1.7334	2.9204	0.2715
		—2.0000**	—0.1667	0.0		0.9800	—2.2466	4.8435	—0.0701
Inia		0.5000	0.5000	0.8333*	—0.1667	—	—1.2000	1.3558	0.8548
		1.0000	0.1667	—0.5000	1.0000		—1.2133	1.2683	1.0144

Generation: F2

Marquis		—	—0.0500	—1.1166	—0.7166	—0.9166	1.8000	3.1762	—0.1594
			—0.2600	—0.2600	—1.5100	—1.1100	2.2267	4.8224	—0.3394
Chinook	Reciprocal effects	—0.3333	—	—0.4667	—0.7333	—0.5167	1.3167	1.6699	—0.1586
		0.1667		—0.6434	0.1900	—1.8267	2.0267	3.9718	0.1459
Khush-hal		—0.4167	—0.4667	—	0.1167	0.3334	—0.3667	0.0707	0.3288
		—0.4167	0.1667		—0.3600	—1.0434	—1.0900	1.0522	—1.1789
Ciano		0.0	0.8333*	0.3333*	—	0.5667	—1.6833	2.7697	0.1956
		—0.4167	—0.2500	—2.2500		1.2066	—2.0066	3.8908	0.4759
Inia		0.0833	0.6667	0.3333	0.4167	—	—1.0067	1.0740	0.3537
		—0.6667	—0.0833	—0.2500	—0.4167	—	—1.1556	1.2020	2.0317

Generation BO

Marquis		—	0.5067	—0.7017	—0.9267	—1.4183	1.8350	3.3042	—0.1577
			—0.1399	0.0351	—0.5150	—1.3733	1.9650	3.7204	—0.3519
Chinook	Reciprocal effects	—0.2917	—	—0.5267	—0.9600	—0.9100	1.1600	1.2825	—0.0721
		—0.5833		0.1100	—1.1483	—0.8816	1.4316	1.9089	—0.3453
Khush-hal		0.0417	—0.4583	—	0.3733	0.3817	—0.1316	—0.0458	0.0989
		—0.1250	—0.6667		—0.2233	0.8050	—0.0350	—0.1395	—0.3474
Ciano		—0.2917	0.3333	0.0417	—	1.1566	—1.5733	2.4122	0.4822
		—0.7083	—0.2083	0.0		0.1600	—2.4850	6.0344	0.1927
Inia		—0.1667	—0.0833	0.0	0.0	—	—1.2899	1.6009	1.2834
		0.0417	0.0	0.1667	—0.0417		—0.8766	0.6277	0.5468

Generation B1

Marquis		—	0.4433	—0.9317	—0.0733	—1.1817	2.0733	4.2302	—0.1713
			0.3217	—0.6616	0.6616	—0.9200	2.3117	5.2404	—0.2584
Chinook	Reciprocal effects	—0.4583	—	—0.8566	—0.8733	—0.1066	1.2483	1.4898	—0.1058
		—0.1667		—0.3617	—0.9617	—0.1617	1.5534	2.3096	—0.2239
Khush-hal		0.5417	—0.2917	—	0.2933	0.5183	—0.5433	0.2267	0.3626
		0.3333	—0.5417		0.4717	0.0217	—0.6300	0.2935	—0.0689
Ciano		0.3333	0.1250	0.4167	—	0.5433	—1.6100	2.5235	0.1134
		0.5000	0.2500	—0.5000		—0.3700	—2.3216	5.2867	0.2494
Inia		0.1667	—0.2500	0.0833	—0.3750	—	—1.1683	1.2965	0.4859
		—0.0417	—0.1250	0.8750	0.1250		—0.9133	0.7308	0.0782

First reading under each column refers to Ellerslie and the second to Parkland

*Significant at 5% level

**Significant at 1% level

Table 2. Estimates of GCA, SCA and RE values and of their variances for the character *final heading*

Generation: F1

♀ Parent		Specific combining ability (SCA) Marquis	Chinook	Khush-hal	Ciano	Inia	GCA	Variance of GCA	Variance of SCA
Marquis		—	1.0733	—0.9267	—1.3600	—1.6000	2.1600	4.5722	—0.2335
			2.9200	—1.7133	—1.4799	—1.4467	—2.4800	5.8774	—0.6322
Chinook		0.0	—	—0.8934	—0.3267	—0.2933	1.7934	3.1227	0.1505
		0.0		—1.6799	—1.2800	—2.0800	2.9466	8.4298	2.2100
Khush-hal	Reciprocal effects	—0.5000	—0.5000	—	—0.4933	—0.1266	—0.3733	0.0459	0.3187
		0.3333	—0.1667		0.2534	0.6200	—1.0867	0.9280	1.2870
Ciano		—0.3333	0.0	0.0	—	0.9400	—2.1066	4.3445	0.4979
		—1.1667	—1.1667	0.0		1.1867	—2.4867	5.9306	0.6655
Inia		0.8333	0.0	0.0	0.0	—	—1.4733	2.0773	0.5436
		0.1667	0.0	0.0	—0.1667		—1.8533	3.1819	2.1050
Generation: F2									
Marquis		—	0.2233	—1.1267	—0.6434	—1.0267	1.9767	3.8498	—0.1441
			1.0167	—1.3833	—1.4333	—1.2333	2.0334	3.9308	—0.5093
Chinook		—0.0833	—	0.3566	—1.0767	—0.2100	1.5767	2.4284	—0.1275
		0.5833		—1.8333	—0.8000	—1.6833	2.5667	6.3842	—0.0158
Khush-hal	Reciprocal effects	—0.0833	—0.6667	—	—0.3434	—0.5600	—0.0733	—0.0523	0.3214
		0.3333	0.2500		0.5167	0.3000	—0.9167	0.6366	1.2490
Ciano		—0.6667	0.6667	0.4167	—	1.2567	—1.9733	3.8362	0.4196
		—0.1667	—0.3333	—0.6667		1.0833	—2.0333	3.9306	0.4779
Inia		0.7500*	0.6667	0.3333	0.4167	—	—1.5066	2.2123	0.8529
		—0.0833		0.3333	—0.6667		—1.6500	2.5188	1.3635
Generation: BO									
Marquis		—	0.8584	—0.5333	—0.2417	—1.7000	2.3333	5.3936	—0.1267
			—0.3133	—0.7883	—0.8883	—0.8967	—1.8967	3.4204	—0.4424
Chinook		—0.2093	—	—0.5416	—0.5000	—0.5000	1.4667	2.1004	0.1189
		—1.0000		—0.2383	—1.1716	—0.9330	2.1800	4.5753	—0.4097
Khush-hal	Reciprocal effects	0.2500	—0.6250	—	—0.4333	0.1917	—0.0166	—0.0504	0.0658
		0.1667	—0.1667		0.6451	0.3450	—0.3450	—0.0579	0.2758
Ciano		—0.2083	0.0833	0.1667	—	0.8584	—1.8500	3.3718	0.0387
		—0.1250	—0.3750	0.6667		0.4117	—2.2034	4.6779	0.4169
Inia		0.3333	0.1667	0.0417	0.1250	—	—1.9333	3.6871	1.1777
		0.2083	0.3750	0.2083	—0.1667		—1.5283	2.1588	0.2101
Generation: B1									
Marquis		—	0.4517	—0.6816	—0.2400	—0.8233	2.2816	5.1591	—0.1169
			0.9417	—1.4000	—0.5167	—0.9250	2.1917	4.6342	—0.4233
Chinook		—1.0417**	—	—0.9817	—0.4983	0.8350	1.4983	2.1983	—0.0489
		—0.5833		—1.4833	—1.3500	—1.2583	2.2334	4.8185	—0.1277
Khush-hal	Reciprocal effects	0.5000	—0.3333	—	0.3683	—0.0483	—0.2433	0.0124	0.3592
		0.1250	—0.0833		1.0167	0.8167	—0.5500	0.1332	0.9634
Ciano		0.6667*	0.7083*	0.7500**	—	0.1433	—2.0183	4.0268	0.0303
		0.5000	0.2917	—0.3750		0.4500	—2.2250	4.7811	0.6177
Inia		1.0833**	—0.4583	—1.2500	—0.2500	—	—1.5183	2.2585	0.3491
		0.2500	0.0417	0.2500	0.0417		—1.6500	2.5532	0.6795

First reading under each column refers to Ellerslie and the second to Parkland.

*Significant at 5 % level
**Significant at 1 % level

Table 3. Estimates of GCA, SCA and RE values and of their variances for the character *heading span*

♀Parent		Specific combining ability (SCA)					GCA	Variance of GCA	Variance of SCA
		Marquis	Chinook	Khush-hal	Ciano	Inia			
Generation: F1									
Marquis		—	2.2533	—1.6133	—0.6133	—0.2133	0.4800	—0.0163	—0.2096
			0.0400	—0.0267	—0.2933	0.1067	0.2600	—0.1184	—0.8721
Chinook		—0.1667	—	—2.0467	—1.5467	—0.9800	0.5800	0.0709	—0.2091
		0.3333		—0.1600	0.0733	0.1400	0.3933	—0.0124	0.8204
Khush-hal		0.5000	—0.1667	—	0.9200	1.4867	—0.2200	—0.0678	—0.2009
		0.0	0.0		—0.6600	—0.5933	0.1267	—0.3004	1.3018
Ciano		0.8333*	0.0	0.0	—	0.3200	—0.2200	0.1097	—0.0340
		0.1667	0.0	—0.6667		—0.0267	—0.4400	—0.3004	—0.3328
Inia		—0.8333*	—0.1667	0.5000	—1.3333**	—	—0.6200	0.0317	—0.0817
		0.3333	—0.5000	—0.8333	0.1667		—0.3400	0.0356	0.2341
Generation: F2									
Marquis		—	0.1667	0.0167	0.1000	—0.0833	0.1500	—0.0443	—0.1671
			0.0200	—1.1133	0.0200	—0.1133	—0.2033	—0.2013	—0.6067
Chinook		0.2500	—	0.7167	—0.4500	0.2000	0.3667	0.0676	—0.1578
		0.4167		—1.1967	—0.9800	0.1367	0.5467	0.0561	—0.6065
Khush-hal		0.3333	—0.2500	—	—0.4333	—0.8667	0.2667	0.0043	0.0042
		0.7500	0.0833		0.8867	1.3367	0.1800	—0.2103	0.2838
Ciano		—0.6667	—0.1667	0.0833	—	0.7167	—0.3167	0.0334	—0.0337
		0.3333	—0.5833	—0.4167		—0.1133	—0.0367	—0.2413	—0.0243
Inia		0.6667	0.0	0.0	0.0	—	—0.4667	0.1509	0.2701
		0.5833	0.2500	0.5833	—0.2500		—0.4867	—0.0058	0.0037
Generation: BO									
Marquis		—	0.2500	0.2000	0.6833	—0.2500	0.4667	0.1601	—0.1442
			—0.2000	—0.7833	—0.3333	0.4500	0.0417	—0.1984	—0.5003
Chinook		0.0833	—	—0.1250	0.3583	0.3000	0.4167	0.1159	—0.1234
		—0.4167		—1.3083	0.0167	—0.0750	0.7750	0.4005	—0.4870
Khush-hal		0.2083	—0.1667	—	—0.7750	—0.1667	0.0917	—0.0493	—0.1257
		0.2917	0.5000		0.6417	0.3000	—0.3500	—0.0776	0.2748
Ciano		0.0417	—0.2500	0.1250	—	—0.2676	—0.3083	0.0374	0.2544
		0.5833	—0.1667	0.3333		0.2917	0.2417	—0.1417	—0.3259
Inia		0.5000	0.2500	0.0417	0.1250		—0.6667	0.3867	—0.0604
		0.1667	0.3750	0.0417	—0.1250		—0.6250	0.1905	—0.3726
Generation: B1									
Marquis		—	—0.0800	0.2867	—0.1300	0.3700	0.1967	—0.0175	—0.1405
			0.6200	—0.6883	—1.1467	—0.0050	—0.1033	—0.1874	—0.4982
Chinook		—0.6550	—	—0.2217	—0.2217	0.8200	0.3717	0.0819	—0.1304
		—0.4167		—1.1217	—0.3717	—1.1467	0.6633	0.3419	—0.3700
Khush-hal		—0.0417	—0.0417	—	0.0200	—0.5217	0.2550	0.0088	—0.0968
		—0.1250	0.4583		0.5283	0.7950	0.0967	—0.1887	0.0821
Ciano		0.3333	0.5833	0.2917	—	—0.3550	—0.4533	0.1493	—0.1089
		0.0	0.0417	0.1250		0.8367	0.0967	—0.1887	0.0822
Inia		0.9167**	—0.2083	—0.3333	0.1250	—	—0.3700	0.0807	0.2620
		0.2917	0.2500	—0.6250	—0.0883		—0.7533	0.3694	0.3871

Reciprocal effects

First reading under each column refers to Ellerslie and the second to Parkland

*Significant at 5% level

**Significant at 1% level

Table 4. Estimates of GCA, SCA and RE values and of their variances for the Character *plant height*

Generation: F1

♀ Parent		Specific combining ability (SCA)					GCA	Variance of GCA	Variance of SCA
		Marquis	Chinook	Khush-hal	Ciano	Inia			
Marquis		—	3.4117	2.0390	—2.3879	—4.1867	13.7470	187.1822	—4.4931
	Reciprocal effects		3.6766	2.7912	—1.9234	—4.4220	12.3968	151.7148	—4.9129
Chinook		0.2933	—	2.4237	1.3784	2.6996	12.1740	146.4086	—0.5994
		—0.1134		1.5132	3.0219	—3.3567	13.4648	179.3356	—0.4071
Khush-hal		—0.4766	0.8250	—	—1.9553	—0.0704	—8.1473	64.5814	—1.1491
		1.2467	1.8566		—0.1367	—0.0287	—8.7599	74 7702	—1.5526
Ciano		—3.7717*	—1.3083	0.9233	—	1.3890	—7.8220	59.3868	—0.6846
		—4.3133	—0.7933	—1.3100		2.0900	—7.9252	60.8436	—0.6295
Inia		5.1567**	—4.5567*	1.0980	—2.0700	—	—9.9516	97.2374	4.4238
		3.3467	—1.4667	2.1400	—0.5600		—9.1766	82.2441	6.8172
Generation: F2									
Marquis		—	2.8015	0.0336	—1.9122	—5.2829	13.3708	177.5788	—2.9988
	Reciprocal effects		1.8702	5.4357	—1.9114	—6.1106	12.9892	166.6538	—5.1606
Chinook		—1.1342	—	1.3486	—3.5393	2.7586	10.0921	100.6507	—0.9129
		2.0642		1.2654	—1.3834	0.2390	13.0445	168 0942	—3.9947
Khush-hal		3.3558*	1.7808	—	1.3133	—0.2195	—6.7329	44.1325	—2.3549
		0.8525	3.4392		0.1846	—2.8154	—7.7827	58.5057	5.2222
Ciano		—0.8783	3.8492*	0.0467	—	1.0260	—7.3467	52.7748	2.9703
		0.0633	5.0650*	0.0592		1.3933	—9.2980	84.3886	—3.2934
Inia		12.9255**	5.8667**	—0.2958	1.5775	—	—9.3831	86.8439	9.5876
		8.2025**	5.3258*	—0.4642	—0.7742		—8.9530	78.0926	10.5941
Generation: BO									
Marquis		—	1.2204	2.4292	0.7733	—5.9562	14.2345	201.2519	—3.4246
	Reciprocal effects		—1.5368	6.4507	3.8329	—4.4574	14.8495	218.5630	—4.8617
Chinook		1.6708	—	0.2537	0.8719	1.8012	9.9832	98.2939	—2.9272
		—0.9280		—0.4441	0.9886	—1.2487	10.2860	103.8567	—4.0744
Khush-hal		2.0138	—1.9303	—	—2.2625	1.5805	—7.6700	57.4592	—1.4352
		1.1430	—2.0403		—1.2273	—0.0541	—8.0976	63.6259	9.0746
Ciano		—2.3949	—2.6567	0.6065	—	0.5592	—6.3678	39.1798	—1.2646
		—1.6303	—1.9159	0.3160		—0.9246	—7.7471	58.0724	0.8631
Inia		4.3464*	2.5614	0.8408	1.1077	—	—10.1798	102.2588	10.4201
		4.2671*	1.7700	—0.0917	0.1983		—9.2909	84.3766	2.5667
Marquis		—	—0.9476	0.7593	2.0884	—3.1655	—3.1655	195.9310	—2.9557
	Reciprocal effects		—0.2117	2.1257	2.3297	—4 4209	—4.4209	155.3739	—3.8799
Chinook		—0.8675	—	—1.0681	0.9945	5.5803	9.8603	96.0433	—2.6564
		1.6562		0.3258	0.1680	2.0856	12.5012	154.7285	3.8664
Khush-hal		2.7857	2.4108	—	0.4511	06493	—8.6035	72.8374	—2.3832
		2.7450	1.8100		2.1056	—0.9884	—8.7700	75.3602	—2.3383
Ciano		5.4176**	0.8667	—0.8083	—	—2.4269	—6.1142	36.2005	—1.1045
		5.5917**	2.7682	0.1045		—1.6792	—7.7160	57.9532	—0.5836
Inia		4.6572**	4.8180**	2.4962	0.4758	—	—9.1824	83.1345	12.8684
		3.6565*	3.6762*	—0.8220	—0.1612		—8.5442	71.4512	5.3504

First reading under each column refers to Ellerslie and the second to Parkland.

*Significant at 5% level
**Significant at 1% level

Table 5. Estimates of GCA, SCA and RE values and of their variances for the character *number* of *tillers per plant*

♀ Parent		Specific combining ability (SCA)					GCA	Variance of GCA	Variance SCA
		Marquis	Chinook	Khush-hal	Ciano	Inia			
Generation: F1									
Marquis		—	—0.0903	—0.7628	0.5342	—0.1946	—0.0409	—0.3273	—0.8224
			—0.8068	—1.2051	—0.3143	—1.1968	0.3351	—0.1992	—0.7787
Chinook		1.1667	—	1.8354	—0.1528	—0.4983	0.8629	0.4155	—0.8197
		0.0667		0.5318	—0.5535	—0.3683	0.3316	—0.2015	—0.5617
Khush-hal		—0.4297	0.1055	—	—0.3790	—0.3183	0.6390	0.0794	0.4944
		1.0167	—0.6833		0.5982	—0 0249	0.5466	—0.0127	—0.2004
Ciano		0.4833	—0.5000	0.7833	—	0.5094	—0.3116	—0.2319	—0.6716
		0.1593	—1.1167	0.6167		1.0399	—0.1349	—0.2933	—0.5244
Inia		—0.4500	—1.2500	0.8227	0.3500	—	—1.1495	0.9923	—0.6077
		0.6000	0.4083	0.4167	—0.7333		—1.0784	0.8513	0.1064
Generation: F2									
Marquis		—	0.0155	—0.5067	0.0520	0.0377	—0.0055	—0.1858	—0.4646
			—0.7810	—0.5043	—0.6510	—0.3043	0.8860	0.5798	—0.5129
Chinook		—0.0833	—	0.4832	—0.9860	0.7246	0.7246	0.4139	—0.4646
		—0.3583		0.9407	—0.2310	—0.2427	0.6827	0.2609	—0.3096
Khush-hal		0.7260	0.5167	—	0.8520	—0.7987	0.4435	0.0108	—0.3012
		1.0667	0.1750		—0.2043	0.1827	0.5310	0.0768	—0.1332
Ciano		—0.4185	0.3667	0.5158	—	0.7167	—0.2707	—0.1126	0.1023
		0.6250	0.8553	—0.0167		0.3123	—0.9973	0.7895	—0.3400
Inia		0.0823	0.7500	0.2437	0.4908	—	—0.5812	0.1520	0.0947
		0.0667	0.1250	0.0333	—0.0500		—1.1023	1.0100	—0.4188
Generation: BO									
Marquis		—	0.0587	0.1659	—0.2478	—0.0077	0.3025	—0.0735	—0.4126
			—0.2333	—0.6416	—0.3376	—0.7573	1.0841	1.0034	—0.4296
Chinook		—0.5267	—	0.2268	0.4683	—0.2315	0.6791	0.2961	—0.4114
		—0.2190		—0.3882	—0.2684	0.0716	0.4932	0.0714	—0.4114
Khush-hal		0.4750	0.0875	—	—0.2497	—0.6937	0.2759	—0.0889	—0.3863
		0.3750	0.2375		0.2336	—0.2010	0.0704	—0.1669	—0.2422
Ciano		—0.1367	—0.5357	0.1792	—	0.4877	—0.2361	—0.1093	—0.2982
		—0.2033	0.2167	—0.1958		0.3607	—0.5536	0.1346	—0.3494
Inia		0.2042	—0.0013	—0.2167	0.6943	—	—1.0213	0.8781	—0.1550
		0.2448	0.0412	—0.0958	0.1668		—1.0940	1.0251	—0.1799
Generation: B1									
Marquis		—	—0.2510	—0.7515	0.5171	0.2983	0.0554	—0.1926	—0.4891
			—0.1161	—0.5486	—0.6927	—1.0161	0.7212	0.3487	—0.4286
Chinook		—0.8792	—	—0.0109	1.0864	—0.1939	0.5642	0.1227	—0.4681
		0.1237		—0.7988	0.2752	0.6594	0.7512	0.3928	—0.4241
Khush-hal		—0.1787	—0.6125	—	0 1419	0.6200	0.3819	—0.0498	—0.3008
		—0.6792	—0.4780		0.7439	0.4993	0.3598	—0.0448	—0.1156
Ciano		0.5208	—0.4260	0.3883	—	—0.6341	—0.0788	—0.1894	0.0001
		1.3028*	0.7470	0.2823		—0.3619	—0.7265	0.3563	—0.0590
Inia		—0.1833	0.3333	0.4685	—0.0167	—	—0.9226	0.6556	—0.1848
		—0.0542	0.5690	—0.2125	0.0857		—1.1017	1.0423	0.1873

Reciprocal effects

First reading under each column refers to Ellerslie and the second to Parkland.

*Significant at 5% level
**Significant at 1% level

Table 6. Estimates of GCA, SCA and RE values and of their variances for the character *number* of *spikelets per spike*

♀ Parent		Specific combining ability (SCA)					GCA	Variance of GCA	Variance of SCA
		Marquis	Chinook	Khush-hal	Ciano	Inia			
Generation: F1									
Marquis		—	—0.2740	0.1741	—0.0388	—0.4728	0.5123	0.1150	—0.3687
			1.1008	—0.2395	—0.1238	—0.1136	0.6729	0.3652	—0.2192
Chinook	Reciprocal effects	—0.3333	—	0.2618	0.3642	—0.0032	0.3536	—0.0224	—0.3436
		0.2668		0.1404	—0.1925	—0.5073	0.4595	0.1235	0.1847
Khush-hal		1.0593	—0 2323	—	—0.3403	—0 1155	—0.5752	0.1834	—0.3357
		—0.3278	—0.3167		0.1615	—0.3017	—0.5058	0.1682	—0.1935
Ciano		—0.0778	—0.1002	0.4888	—	0.2157	—0.3151	—0.0482	—0.2854
		—0.4012	—0.0277	0.2057		0.5208	—0.3616	0.0431	—0.1931
Inia		—0.4388	0.1947	0.4692	0.0222	—	0.0245	—0.1469	—0.2742
		—0.2390	0.3458	0.1447	—0.2168		—0.2650	—0.0175	—0.0073
Generation: F2									
Marquis		—	—0.0184	0.3592	—0.2315	—0.0934	0.7264	0.4810	—0.1169
			0.5606	0.1479	0.1164	—0.1162	0.6867	0.4044	—0.1677
Chinook	Reciprocal effects	0.8083*	—	—0.0646	—0.1672	0.5422	0.2257	0.0042	—0.1168
		0.0222		0.4920	—0.3278	—0.1107	0.4672	0.1512	—0.0629
Khush-hal		—0.2523	—0.0500	—	0.3346	—0.5709	—0.6356	0.3537	—0.0725
		—0.0472	0.3832		—0.3072	—0.1203	—0.3060	0.0266	—0.0796
Ciano		—0.0117	0.1972	0.2123	—	0.1788	—0.4576	0.1626	—0.0524
		—0.0870	—0.2613	0.2750		0.2484	—0.7084	0.4348	—0.0959
Inia		0.4678	0.1057	—0.3205	—0.1243	—	0.1412	—0.0268	0.1033
		0.3723	0.0473	0.1305	0.0418		—0.1394	—0.0476	—0.1337
Generation: BO									
Marquis		—	0.3819	0.2495	—0.0846	—0.3061	0 8035	0.6124	—0.0831
			0.1083	0.4159	0.0875	—0.0067	0.6312	0.3646	—0.0845
Chinook	Reciprocal effects	—0.0993	—	0.1926	—0.0259	—0.1115	0.2629	0.0359	—0.0345
		0.0138		—0.3419	0.2164	0.1788	0.2373	0.0215	—0.0805
Khush-hal		0.4042	—0.1623	—	0.1214	—0.0359	—0.4382	0.1588	—0.0500
		0.1975	—0.1708		0.0086	0.0971	—0.3260	0.0725	0.0122
Ciano		—0.2898	—0.1850	0.0875	—	0.0676	—0.5110	0.2279	—0.0756
		0.1233	0.2027	0.1573		—0.1626	—0.5021	0.2183	—0.0663
Inia		0.0335	0.0988	0.1557	0.1650	—	—0.1172	—0.0195	—0.0457
		0.3435	0.3020	0.0598	—0.0790		—0.0404	—0.0322	—0.0618
Generation: B1									
Marquis		—	0.0734	0.0484	0.2291	—0.1514	0.7318	0.5031	—0.0810
			0.5629	0.1757	—0.0347	—0.0883	0.5099	0.2252	—0.0870
Chinook	Reciprocal effects	—0.1043	—	—0.0157	0.5060	—0.3085	0.1207	—0.0178	—0.0792
		0.2835		—0.0718	—0.0863	0.1980	0.3313	0.0750	0.0186
Khush-hal		0.2930	0.2042	—	0.1958	0.3165	—0.4789	0.1969	—0.0801
		0.2293	0.0835		0.3633	0.0295	—0.2941	0.0517	—0.0750
Ciano		0.5625*	—0.0867	0.0905	—	—0.1931	—0.2321	0.0215	0.0346
		0.4038	0.4050	0.4162		0.1860	—0.4894	0.2047	—0.0402
Inia		—0.1140	0.3238	0.1035	—0.4457	—	—0.1415	—0.0124	0.0041
		0.1040	0.0657	0.0598	—0.2070		—0.0577	- 0.0315	—0.0595

First reading under each column refers to Ellersalie and the second to Parkland.

*Significant at 5% level

**Significant at 1% level

Table 7. Estimates of GCA, SCA and RE values and of their variances for the character *number of seeds per spike*

Generation: F1

♀ Parent		Specific combining ability (SCA)					GCA	Variance of GCA	Variance of SCA
		Marquis	Chinook	Khush-hal	Ciano	Inia			
Marquis		—	—1.9659	2.2792	0.9872	—3.1363	2.8305	6.6103	—3.5029
			1.2486	0.1486	—1.2352	1.7185	2.0515	3.1165	—2.7300
Chinook		—0.6665	—	0.0151	0.9075	2.0447	—1.5451	0.9862	—2.2146
		0.1168		0.1197	—0.3172	0.1696	—0.9495	—0.1904	—2.2104
Khush-hal		3.1140	—1.3513	—	—2.5752	—0.3525	—1.1460	—0.0878	—1.7712
		1.5667	—0.7168		—0.1725	—2.4527	0.3450	—0.9730	—2.2186
Ciano		4.5557**	1.7223	—0.6055	—	2.9756	—1.9094	2.2445	—0.6930
		0.4772	0.5945	1.0333		1.9031	—2.4385	4.8542	—2.1780
Inia		—1.5222	0.0723	—0.7965	—2.2833	—	1.7700	1.7317	4.1624
		—1.1278	1.5223	—0.8835	—1.1335		—0.9916	—0.1088	1.4764

Reciprocal effects

Generation: F2

Marquis		—	1.1545	—0.7005	0.1160	0.5999	3.1883	9.3728	—1.9670
			0.2870	—0.0244	1.3941	0.6768	2.2384	4.0955	—2.2876
Chinook		0.7028	—	0.0982	—0.0284	2.0048	—1.5763	1.6979	—1.5227
		0.1278		0.0492	—0.1192	0.7419	—1.1155	0.3293	—2.2601
Khush-hal		0.1287	—1.4832	—	0.2428	—1.4129	—1.7061	2.1238	—1.8002
		—1.2997	0.0360		—1.8748	—0.5793	0.2738	—0.8401	—2.2866
Ciano		0.7217	0.9697	—0.1442	—	1.3696	—3.1989	4.0483	—1.9426
		0.7168	—1.2167	0.3277		0.7678	—2.4832	5.2511	—0.4635
Inia		1.7125	—0.0612	1.0087	0.5783	—	2.2930	4.4710	0.7809
		0.9752	0.4083	—0.7652	1.0390		1.0865	—0.2653	—1.6431

Reciprocal effects

Generation: BO

Marquis		—	0.1015	0.0655	0.4011	—1.3428	3.5835	12.0552	—1.9664
			0.2519	0.1132	0.8717	0.3590	2.0422	3.7491	—1.0532
Chinook		0.1910	—	—0.3113	0.0544	0.0701	—1.8660	2.6953	—1.9630
		—0.6400		—1.5280	0.2122	1.3177	—1.2955	1.2570	—1.0321
Khush-hal		0.8403	—0.7640	—	—0.9921	0.2122	—1.1196	0.4670	—1.9327
		0.7335	0.4013		—0.8981	0.0125	0.5107	—0.1605	—0.2707
Ciano		—1.1300	—1.0005	—0.5227	—	1.8083	—2.1986	4.0471	—1.5837
		0.7405	0.4957	1.0112		—0.2557	—2.4295	5.4813	—0.5161
Inia		—0.4867	0.0820	—0.2068	—1.2177	—	1.6006	1.7754	—0.2588
		0.3572	0.0558	0.3265	—0.5962		1.1722	0.9527	—0.4097

Reciprocal effects

Generation: B1

Marquis		—	—0.7567	0.5266	1.6680	—1.1312	3.7367	13.2888	—1.6858
			1.1823	0.3948	1.0759	—0.8422	1.8352	2.9362	—1.0793
Chinook		—0.6193	—	—1.5155	1.7828	0.5295	—2.1908	4.1253	—1.4949
		0.3758		—0.9669	0.2750	1.0215	—1.0805	0.7357	—0.6134
Khush-hal		2.2568*	0.6265	—	—0.6317	1.1138	—1.2477	0.8823	—0.8277
		0.4473	1.2037		—0.6815	—0.3786	0.4308	—0.2461	—0.7157
Ciano		3.6903**	1.2785	0.1728	—	0.4189	—1.6029	1.8950	—0.4341
		1.9765	2.0132	1.6680		1.2470	—1.8508	2.7759	—0.5141
Inia		—0.1847	1.2072	—1.7647	—1.2285	—	1.3047	1.0280	—0.6937
		0.1222	—0.5362	—0.0292	1.0437	—	0.6653	0.0109	—0.0279

Reciprocal effects

First reading under each column refers to Ellerslie and the second to Parkland.

*Significant at 5% level
**Significant at 1% level

Table 8. Estimates of GCA, SCA and RE values and of their variances for the character *weight of seeds per spike*

Generation: F1

♀ Parent		Specific combining ability (SCA)					GCA	Variance of GCA	Variance of SCA
		Marquis	Chinook	Khush-hal	Ciano	Inia			
Marquis		—	—0.0905	0.0739	0.1517	—0.1100	- 0.0103	- 0.0032	—0.0083
			0.0512	—0.0038	0.0746	0.0983	—0.0326	- 0.0027	—0.0095
Chinook		—0.0175	—	0.0364	0.0412	0.4039	—0.1285	0.0132	—0.0056
		—0.0320		0.0194	—0.0762	0.0399	—0.0958	0.0054	—0.0087
Khush-hal		0.1782*	—0.0788	—	—0.1029	0.0727	—0.0092	—0.0033	—0.0061
		- 0.0287	— 0.0527		0.0249	— 0.0356	0.0846	0.0034	—0.0094
Ciano		0.2843**	0.0267	—0.0705	—	0.0391	0.0008	—0.0033	0.0036
		0.0622	0.0268	0.1142		0.0487	- 0.0501	—0.0013	—0.0055
Inia		—0.0590	—0.1433	0.0425	—0.0505	—	0.1472	0.0183	—0.0014
		—0.0805	—0.0038	0.0427	—0.0460		0.0938	0.0050	—0.0046

Reciprocal effects

Generation: F2

Marquis		—	—0.0530	0.0072	0.0107	0.1000	0.0283	—0.0017	—0.0064
			0.0068	—0.0384	0.0898	0.1372	—0.0274	—0.0018	—0.0063
Chinook		0.0022	—	—0.0560	0.0218	0.0196	—0.1592	0.0228	—0.0054
		0.0172		—0.0018	—0.0060	—0.0131	—0.1023	0.0079	—0.0063
Khush-hal		—0.2083	—0.0740	—	0.0447	—0.0299	—0.0475	—0.0003	—0.0053
		—0.0558	—0.0208		—0.0383	0.0114	0.0665	0.0019	—0.0058
Ciano		0.1072	0.0355	—0.0413	—	—0.0030	—0.0079	—0.0025	—0.0055
		0.0700	—0.0573	—0.0225		0.0051	—0.0431	—0.0007	—0.0031
Inia		0.2037	0.0072	—0.0377	—0.0052	—	0.1863	0.0322	—0.0026
		0.0885	—0.0143	—0.0503	0.0277		0.1063	0.0088	0.0001

Reciprocal effects

Generation: BO

Marquis		—	0.0490	—0.0080	—0.0624	—0.0289	- 0.0059	—0.0029	—0.0074
			0.0461	—0.0314	0.0606	0.0699	—0.0342	—0.0004	—0.0039
Chinook		0.0552	—	—0.0406	—0.0150	—0.0264	—0.1185	0.0111	—0.0066
		0.0048		—0.0746	0.0018	0.0180	—0.0813	0.0050	—0.0032
Khush-hal		0.0022	—0.0190	—	0.0007	0.0178	—0.0222	—0.0025	—0.0068
		0.0150	0.0120		—0.0103	—0.0050	0.0577	0.0018	—0.0017
Ciano		—0.0810	—0.0268	—0.0028	—	0.0589	—0.0306	—0.0220	—0.0068
		0.0340	0.0335	0.0553		—0.0137	—0.0309	—0.0006	—0.0027
Inia		—0.0638	0.0252	—0.0277	—0.0955	—	0.1771	0.0284	—0.0056
		—0.0573	—0.0090	0.0240	- 0.0190		0.0888	0.0063	—0.0021

Reciprocal effects

Generation: B1

Marquis		—	0.0198	0.0027	0.0572	—0.0088	—0.0230	—0.0013	—0.0045
			0.0547	0.0141	0.0700	0.0494	—0.0314	—0.0005	—0.0039
Chinook		0.0158	—	—0.0387	0.0596	—0.0314	—0.1290	0.0148	—0.0044
		0.0358		—0.0251	0.0011	—0.0083	—0.0845	0.0056	—0.0030
Khush-hal		0.0618	0.0010	—	—0.0354	0.0368	—0.0362	—0.0005	—0.0040
		0.0115	0.0585		—0.0536	0.0111	0.0607	0.0021	—0.0037
Ciano		0.0885	0.0058	—0.0500	—	—0.0179	—0.0017	—0.0018	—0.0018
		0.0322	0.0608	0.0683		0.0659	—0.0282	—0.0008	—0.0013
Inia		—0.0882	0.0082	—0.0368	—0.0763	—	0.1439	0.0189	—0.0036
		—0.0605	—0.0293	—0.0732	—0.0942		0.0834	0.0054	—0.0016

Reciprocal effects

First reading under each column refers to Ellerslie and the second to Parkland.

*Significant at 5% level
**Significant at 1% level

Table 9. Estimates of GCA, SCA and RE values and of their variances for the character 1000-*kernel weight*

Generation: F1

♀ Parent		Specific combining ability (SCA)					GCA	Variance of GCA	Variance of SCA
		Marquis	Chinook	Khush-hal	Ciano	Inia			
Marquis		—	—0.1201	—0.5650	2.0236	0.1734	—2.4230	—1.0311	—2.6455
			0.0835	—0.2523	2.6151	0.8063	—2.3256	—0.2340	—1.2556
Chinook		0.2312	—	0.7965	0.0375	—0.7600	—1.5338	0.4628	—2.5316
		—0.7130		0.3194	—1.5360	0.9759	—1.3217	—0.2366	—1.2425
Khush-hal		1.1725	—0.6182	—	0.0280	1.8405	0.7291	—1.0567	—1.1211
		—1.7405	—0.4882		0.7257	1.4420	1.6523	—0.3825	—1.2450
Ciano		2.1175	—0.9577	—1.2283	—	—1.5895	1.7007	—1.0220	—0.6646
		1.0338	0.1613	1.7450		—0.4875	0.8898	—0.4331	—0.9974
Inia		—0.0403	—3.1908*	1.4478	0.8910	—	1.5269	0.4939	—1.2788
		—0.0033	—1.3335	1.8997	0.0420		1.1052	—0.3636	—0.9555

Reciprocal effects

Generation: F2

Marquis		—	—0.0159	0.2364	—0.1336	1.4490	—2.0321	3.4447	—1.7115
			—0.2108	—0.8323	1.4480	2.2354	—2.2536	4.5162	—1.4056
Chinook		—0.5203	—	—1.4490	0.4314	—1.1334	—2.2150	4.3318	—1.7114
		0.2470		0.1446	—0.2289	—0.7060	—1.3656	1.3026	—1.3909
Khush-hal		—1.2750	—0.4182	—	0.9701	0.9718	0.4223	—0.5063	—0.9926
		—0.2907	—0.5318		0.3904	0.9605	1.2445	0.9866	—1.1678
Ciano		1.6177	0.0647	—1.0387	—	—1.8572	—1.7856	2.5039	—1.3299
		0.2192	—0.3352	—0.0517		0.3992	1.2144	0.9125	—0 6385
Inia		—0.7592	0.1358	—0.8753	—0.6647	—	2.0392	3.4739	0.3453
		1.0892	—0.5033	—0.2993	0.3512		1.1603	0.7840	0.7868

Reciprocal effects

Generation: BO

Marquis		—	0.6721	—0.3252	—0.8322	0.3192	—2.6314	6.4507	—1.1837
			0.8088	—0.7960	0.4879	1.4128	—2.3445	5.0647	—1.0796
Chinook		0.9477	—	—0.5640	—0.4496	—0.4911	—1.2960	1.2062	—1.0332
		0.4982		—0.5859	—0.1117	—0.5019	—0.7879	0.1889	—0.8615
Khush-hal		—0.5490	0.3412	—	0.5533	0.3476	0.3155	—0.3740	—1.0425
		—0.1602	0.0255		0.8728	—0.0248	0.9186	0.4120	—0.7540
Ciano		0.5182	0.1213	. 0.5002	—	—0.5193	1.4580	1.6523	—0.7835
		0.4008	0.3108	—0.0305		—0.1230	1.4448	1.6556	—0.7422
Inia		—0.8622	0.5862	—0.1982	—0.7360	—	2.1540	4.1662	—0.9392
		—1.3710	—0.2628	0.2245	—0.0462		0.7690	0.1496	—0.3250

Reciprocal effects

Generation: B1

Marquis		—	0.1205	—0.4528	—0.2338	0.7582	—2.3425	5.0186	—1.1713
			0.3031	0.0634	0.5471	1.7552	—2.0504	3.8294	—0.9369
Chinook		0.6497	—	0.4032	—0.1392	—1.1356	—1.1454	0.8434	— 1.1665
		6.4662		0.0455	—0.2633	—0.8131	—1.0151	0.6557	—0.9063
Khush-hal		—0.2560	—0.3190	—	—0.3410	0.0372	0.2448	—0.4096	—1.0488
		—0.0027	0.5133		0.5745	0.2047	0.9964	0.6180	—0.9325
Ciano		—0.9073	—0.9833	—1.1687	—	—0.8553	1.4072	1.5116	—1.1070
		—0.8827	—0.2765	0.1982		0.5392	0.9224	0.4760	—0.7040
Inia		—1.5043	—0.5807	0.6037	—0.5812	—	1.8379	2.9294	—0.3055
		—1.1452	—0.1232	—1.6265	—1.2087	—	1.1468	0.9405	0.4212

Reciprocal effects

First reading under each column refers to Ellerslie and the second to Parkland.

* Significant at 5% level

**Significant at 1% level

Table 10. Estimates of GCA, SCA and RE values and of their variances for the character *yield per plant*

Generation: F1

♀ Parent		Specific combining ability (SCA)					GCA	Variance of GCA	Variance of SCA
		Marquis	Chinook	Khush-hal	Ciano	Inia			
Marquis		—	—0.5845	—0.9024	2.4220	—0.3343	—0.1646	—1.0311	— 2.6455
	Reciprocal effects		- 0.1980	0.1755	0.8520	0.0911	—0.4672	—0.2840	—1.2556
Chinook		1.1575	—	1.9387	0.0545	—0.7460	—1.2330	0.4628	—2.5316
		—0.6980		0.0337	—0.2106	—0.6938	—0.5154	—0.2366	—1.2425
Khush-hal		0.3260	—0.7188	—	—0.2716	1.6500	—0.0382	—1.0567	— 1.1211
		—0.1923	- 0.5447		—0.0804	0.2976	0.3461	—0.3825	—1.2450
Ciano		2.5833	—0.5388	0.8368	—	—0.9329	0.1903	—1.0220	—0.6646
		—2.0633*	—0.3382	1.6012		0.5674	0.2629	—0.4331	—0.9974
Inia		—0.2452	—3.2108*	0.5890	0.5675	—	1.2458	0.4939	—1.2788
		—1.0785	—0.0700	2.5692*	—0.4895		0.3736	—0.3636	- 0.9555

Generation: F2

Marquis		—	0.5420	—0.8646	1.1590	—0.1661	0.0508	—0.3966	—0.9980
	Reciprocal effects		—0.8039	0.7455	0.0267	0.7448	—0.5307	—0.1445	—1.0655
Chinook		—0.4107	—	0.1680	—1.0782	0.1929	—1.4712	1.7653	—0.9001
		0.6045		1.3541	—0.7700	0.3538	0.1256	—0.4104	—0.8501
Khush-hal		2.1502*	0.5530	—	1.7764	—0.4546	—0.7275	0.1300	—0.7394
		—1.5562	—0.0635		0.0255	- 1.2061	0.6319	—0.0270	—0.2690
Ciano		- 0.9003	—0.1892	—0.4672	—	0.6059	0.6961	0.0854	0.8891
		1.3395	—0.1583	—0.2452		0.1652	—0.5374	—0.1373	—0.8674
Inia		1.0152	1.1928	0.6962	—0.4528	—	1.4518	1.7084	—0.9061
		0.5628	—0.4918	—0.3988	—0.1468		0.3109	—0.3296	—0.3448

Generation: BO

Marquis		—	0.5268	0.1073	—0.2387	- 0.6415	0.0570	—0.3228	—0.8150
	Reciprocal effects		0.6335	—0.0471	—0.3599	0.0177	—0.4831	0.0377	—0.4891
Chinook		0.7010	—	0.6673	—0.0782	—0.6920	—0.7077	0.1748	—0.7225
		—0.4425		—0.6144	—0.2531	0.0680	0.2577	—0.1292	—0.3553
Khush-hal		0.3322	—0.1002	—	0.2599	—1.2433	—0.6801	0.1365	—0.6627
		0.1092	0.6103		0.5103	—0.7849	—0.0136	—0.1995	—0.3625
Ciano		—0.3313	—0.8415	0.7498	—	0.3511	0.3461	—0.2062	—0.7715
		0.5293	0.0917	0.6003		0.0547	—0.0030	—0.1956	—0.3378
Inia		—0.6825	0.2547	—0.4963	1.1603	—	0.9848	0.6438	0.0374
		—0.8422	0.7200	0.0107	0.1920		0.2419	—0.1371	—0.2811

Generation: B1

Marquis		—	—0.7261	—0.3666	0.7549	0.5342	—0.0471	—0.2104	—0.5317
	Reciprocal effects		0.5455	0.4427	0.1542	0.1742	—0.5386	0.0529	—0.5930
Chinook		—0.7872	—	0.0090	2.2304	—0.7179	—0.8473	0.5052	—0.3559
		0.9510		—1.0145	0.3140	0.4450	0.0681	—0.2316	—0.4939
Khush-hal		0.4678	—0.4883	—	0.2590	0.3710	—0.7653	0.3731	—0.4868
		0.0278	0.3863		0.4008	0.7432	0.3231	—0.1328	—0.1846
Ciano		- 0.3572	—0.6105	0.1253	—	—1.7105	0.6451	0.2034	1.3389
		0.7125	0.7283	1.4295*		—1.7015	—0.2341	—0.1824	—0.4987
Inia		—0.1232	—0.2025	—0.0010	0.0565	—0.5442	1.0147	0.8169	0.7462
		0.2093	0.5000	—0.4568	—0.1675		0.3815	—0.0917	—0.2341

First reading under each column refers to Ellerlie and the Second to Parkland.

* Significant at 5% level

**Significant at 1% level

Table 11. Analysis of variance of general and specific combining ability and reciprocal effects (RE) from four diallel generation for ten characters at two locations

Character	F_1 - diallel			F_2 — diallel			Backcross diallel			Selfed backcross diallel		
	M.S. for GCA	M.S. for SCA	M.S. for RE	M.S. for GCA	M.S. for SCA	M.S. for RE	M.S. for GCA	M.S. for SCA	M.S. for RE	M.S. for GCA	M.S. for SCA	M.S. for RE
Onset of-heading	26.343**	1.912**	0.455	22.703**	2.118**	0.400	22.140**	2.550**	0.105	25.265**	1.506**	0.225
	41.935**	2.231**	1.272	39.046**	4.006**	0.243	22.410**	2.387**	0.275	35.937**	1.043*	0.358
Final heading	36.500**	2.856**	0.261	31.375**	2.306**	0.562*	36.859**	1.768**	0.146	34.687**	0.050**	0.892
	64.046**	7.131**	0.316	46.000**	5.681**	0.337	39.125**	3.837**	0.382	44.375**	3.856**	0.193
Heading-span	1.368**	0.495**	0.333	1.365*	0.527*	0.231	2.348**	0.542*	0.097	1.460**	0.403	0.388
	2.619	4.581**	0.750	1.526	1.958*	0.434	2.934**	1.238	0.234	2.592**	1.905	0.192
Plant Height	1409.406**	22.800**	14.125*	1169.937**	17.706**	47.074**	1263.187**	13.868**	10.223	1225.093**	13.593**	19.286**
	1396.734**	22.625**	8.677	1415.109**	25.225**	27.787	1345.468**	26.506**	6.829	1306.546**	13.637*	16.016**
Number of tillers per plant	6.432**	1.221	1.043	1.950*	0.880	0.583	4.322**	0.336	0.283	3.313**	0.768	0.429
	4.258**	2.633	0.879	9.358**	1.098	0.489	7.319**	0.902	0.094	7.385**	1.349*	0.683
Number of spiklets per spike	2.045*	0.208	0.401	3.032**	.206	0.230	2.955**	0.143	0.077	2.135**	0.226	0.158
	2.802**	0.503	0.145	3.262**	0.278	0.092	2.039**	0.128	0.073	1.750**	0.241	0.140
Number of seeds per spike	46.28**	9.321	8.844	64.140**	3.382	1.696	62.421**	1.652	1.129	61.468**	3.657	5.453*
	30.406**	4.400	2.057	34.203**	2.978	1.318	33.384**	2.171	0.703	21.484**	2.880	2.784
Weight of seeds per spike	0.095**	0.016	0.030*	0.157**	0.006	0.004	0.117**	0.003	0.004	0.098**	0.003	0.005
	0.071**	0.013	0.006	0.072*	0.012	0.004	0.049**	0.007	0.002	0.048**	0.009	0.006
1000-kernel weight	34.953**	3.026	4.358	41.406**	2.657	1.514	38.687**	0.800	0.703	30.546**	1.094	1.409
	29.750**	5.250	2.862	28.281**	3.353	0.448	24.105**	1.576	0.506	21.003**	2.025	1.361
Yield per plant	7.848	3.807	4.132	13.222**	1.869	1.872	5.145**	1.214	0.725	6.878**	2.562**	0.330
	2.033	0.697	3.152	2.710	1.324	1.082	0.900	0.507	0.501	1.499	0.743	0.933

The first reading under each column refers to Ellerslie and the second to Parkland.

*Significant at 5% level
**Significant at 1% level

Table 12. Factorial analysis of variance of general combining ability over four generations and two locations.

Source of variation	D.F.	Sum of squares	Mean squares	F ratio
Locations	1	1.71959	1.71959	1.15079
Parents (P)	4	2.54764	0.63691	0.42623
L × P	4	1.11852	0.27963	0.18713
Generations (G)	3	4.27284	1.42428	0.95316
L × G	3	1.78580	0.59526	0.39837
P × G	12	6.27137	0.52261	0.34975
L × P × G	12	3.89558	0.32463	0.34975
Error	360	537.93774	1.49427	—
Locations (L)	1	1.71929	1.71959	1.88320
Parents (P)	4	2.54764	0.63691	0.69752
L × P	4	1.11852	0.27963	0.30624
Generations (G)	3	4.27284	1.42428	1.55981
L × G	3	1.78580	0.59526	0 65191
P × G	12	6.27137	0.52261	0.57234
L × P × G	12	3.89558	0.32463	0.35552
Characters (C)	9	12.89835	1.43315	1.56952
L × C	9	8.39085	0.93331	1.02213
P ×C	36	91.33239	2.53701	2.77842***
G × C	27	21.10522	0.78167	0.85606
L × P × C	36	192.26447	5.34067	5.84888***
L × G × C	27	21.24818	0.78696	0.86185
P × G × C	108	92.07365	0.85253	0.86185
Error (L × P × G × C)	108	98.61607	0.91311	—

***Significant at 0.1 % level.

Table 13. Analysis of variance of Parkland GCAs' regression upon Ellerslie GCAs' regression for each of the parental lines.

Parent	Source of variation	D.F.	Sum of squares	Mean squares	Regression coefficient
Marquis	Due to regression	1	157.5731	157.5731***	
	Due to error	8	1.8675	0.2334	b=0.9416
Chinook	Due to regression	1	138.6222	138.6222***	
	Due to error	8	1.3375	0.1671	b=1.1118
Khush-hal	Due to regression	1	62.7426	62.7426***	
	Due to error	8	4.2024	1.5253	b=1.0769
Ciano	Due to regression	1	60.1871	60.1872***	
	Due to error	8	1.0378	0.1297	b=1.1163
Inia	Due to regression	1	75.7396	75.7396***	
	Due to error	8	.4692	0.0586	b=0.8821

***Significant at 0.1 % level

Table 14. Summary of the results of General and Specific combing ability analyses showing that the hybrids with hybrids SCA's are associated with parents of low GCA's and Vice Versa.

		Onset-of-heading				Final heading				Heading-span				Plant height				Number of tillers per plant			
		F1	F2	B0	B1	F1	F2	B0	B1	F1	F2	B0	B1	F1	F2	B0	B1	F1	F2	B0	B1
Hybrid with highest SCA	Both parents with high GCA									+ −				+ −	+ −			+ −			
	One parent with low GCA				− +	− +			− +	− +	+ +	+ +	+ −		− +	− +	− +		+ +		+ +
	Both parents with low GCA	+ −	− −	+ −	+ −		+ +	+ +	− −									− −		+ −	
Hybrid with lowest SCA	Both parents with high GCA				+ +									− +	+ +			− +			
	One parent with high GCA	+ +	+ +	+ −		+ −	+ −	+ +	+ +	+ +	+ +	+ +	+ +			+ +	+ +	+ −	+ −	+ +	+ +
	Both parents with low GCA																				

		Number of spikelets per spike				Number of seeds per spike				Weight of seeds per spike				1000-kernel weight				Yield per plant			
		F1	F2	B0	B1	F1	F2	B0	B1	F1	F2	B0	B1	F1	F2	B0	B1	F1	F2	B0	B1
Hybrid with highest SCA	*Both parents with high GCA	− −	− −	+ −	− −																
	One parent with low GCA	+ −	− −	− +	+ −			+ −		− +	+ −	+ −		− +	+ +	+ −	+ −	+ +	− −	− +	− −
	Both parents with low GCA					+ −	+ −	− +	+ −	− −			− +							+ −	
Hybrid with lowest SCA	Both parents with high GCA					+ −								+ −	+ −			+ −	− +		
	One parent with high GCA	+ −	+ −	− −	+ +	+ +		+ −	− +	+ −	− −	− +	+ −	− +	− +	+ +	+ +	− −	+ −	− −	+ +
	*Both parents with low GCA									− −	+ −	+ −	+ −								

(+) and (−) signs indicate, respectively, affirmation and contradiction of the statements.
The first position of (+) or (−) refers to Ellerslie and the second to Parkland.
*(+) sign characteristic of the location shows disagreement of the proposition made in the text.
F1, F2, B0 and B1 refer to F_1, F_2, backcross and selfed backcross generations of diallel set.

The factorial ANOVA of GCA's is given in Table 12. The first part of Table 12 shows a three-way layout analysis where locations, parents and generations have been treated as the main effects. None of the mean squares showed significance. This means that parental lines did not differ in their general combining abilities over the two locations in any generation of the diallel cross. When the characters were introduced as fourth main effect and the normalized GCA's analysed in a four-way factorial layout (second part of Table 12), the mean squares for P×C and L×P×C interactions were significant. This suggests that the combining ability values for different characters vary with the number of parents and locations.

It is interesting to note that after introducing characters as separate effects, the mean squares either for generations or any of the interactions involving generations, were not significant. This indicates that diallel generations do not affect GCA's for any character in question. The significance of P×C and L×P×C interaction on the other hand provides the possibility of comparing which of the parental lines, for their relative adaptability, is more adaptive with respect to two locations. For this purpose, the GCA's for all the characters (averaged over all the generations), at Parkland were regressed for each of the parental line upon those at Ellerslie. The regression coefficients and the sum of squares due to regression and error, partitioned for each of the cultivar, are given is Table 13. It may be pointed that unweighted GCA's were used in the regression analysis since the effect of change in the degree of expression of one character relative to the other can be studied regardless of the unit of scale used. Significance of mean squares due to regression (Table 13) indicates that for every unit of change in GCA's at Ellerslie there is a corresponding proportional change for the corresponding GCA's at Parkland. In other words the inter-location environmental effects with respect to each of the cultivars are fairly homogeneous.

Discussion

The F_1, F_2, backcross and selfed backcross generations of a five parent diallel cross of common wheat (*Triticum aestivum* L.) grown in 1972 at two locations were analysed with respect to general and specific combining abilities and inter-location environmental effects. The results of the analysis of the data with respect to characters considered have shown that the parents with high GCA do not necessarily produce hybrids with high SCA . The comparisons of GCA's with SCA's for all the generations and characters are shown in Table 14. Of all the comparisons, eighty to be exact, in 84% of the cases high SCA's of the hydrids are associated with one or both parents of low GCA's and *vice versa*. These observations are in agreement with those reported by Crumpacker & Urquhart (1962), Fonseca (1965), Brown *et al* (1966), Gyawali *et al* (1968) and Singh *et al* (1969) in wheat. Analogous results have also been reported by Larson (1941) in tomato: Walker (1963), Chang (1967), Soomro (1967), Baluch & Soomro (1969) and Soomro & Baluch (1969) in cotton.

Significant variances for general and specific combining abilities for a particular character, respectively, denote the importance of additive and non-additive gene effects for that character. If the variance for specific combining ability for a particular character is significant and that for general combining ability it is not, selection for that character will be on the basis of SCA. On the other hand, high SCA variances associated with a particular parent, even if it has high SCA, reflect an inconsistency in the performance of that parent with respect to the particular character (Griffing 1956) and indicate that the hybrids involved with that parent would perform poorer than would be expected on the basis of their specific combining abilities. It follows,

therefore, that in combining ability screening tests, a pedigree selection procedure would be expected to screen out the strains with considerably larger SCA variances.

In the present studies variances for general combining ability were generally larger than those for specific combining ability for all the characters and diallel generations at both locations (Table 1 to 10). There were a few cases where the estimates of SCA variances were higher than those for GCA's, but the magnitude of their differences were negligible. This would indicate a high consistency of performance of the parental lines, an observation which may also be generally verified by their general combining ability values and more specifically from the results of Table 13. The significance of variances for general and specific combining abilities was examined from Tables 1 to 10. In general, the mean squares for GCA were significant for all characters except heading-span and yield per plant at one or both the locations. Such significance of GCA mean squares are not uncommon in wheat (Fonseca 1965, Brown *et al.*, 1966, Paroda & Joshi 1970, Parodi *et al.*, 1970; Bitzer *et al.*, 1971). Mean squares for SCA were significant only for a few characters.

In the factorial ANOVA for general combining abilities of four generations of diallel cross over two locations (Table 12), it was found that GCA values were more or less the same. However when characters were treated separately in the analysis (ANOVA assumed single observation per cell), GCA's differed between locations. These results indicate that parents did not differ in GCA's over the two locations when their GCA's were averaged over all characters, but they certainly did when considered individually for each character. The responses of each variety with respect to additive gene effects was studied after averaging the GCA's of cultivar over four generations of diallel cross and regressing the estimates obtained at one location upon those of the other. In the analysis of variance for regression, the inter-location effects were found to be homogeneous for each variety. In other words the GCA's for the two locations were concordant. The variances of general and specific combining ability also did not differ significantly at the two locations. Moreover, the conspicuous feature of the combining ability analysis was the high consistency with which the GCA variances were higher than the corresponding SCA variances at both locations. This in fact shows the stability of cultivars over locations according to Griffing (1956).

It will not be out of place to mention here that a high general combining ability for some characters for example onset-of-heading and final heading may not be desirable under certain circumstances. High GCA for these characters implies lateness, so that when selecting for earliness, lines with the lowest GCA's must therefore be given perference. In the present study Ciano and Inia had the lowest GCA's for heading data, and consequently selection from their progenies is expected to result in early lines. Plant height is another character for which the selection of wheat cultivars with low GCA's is desirable.

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