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Parental Generation in Relation to Combining Ability Analysis in Spring Barley

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Summary. A comparison between Griffing's (1956) Method 1, Model I, and Method 3, Model I, using data from a 10 × 10 diallel of spring barley grown in eight different environments, revealed that inclusion of the parental generation (Method 1) caused considerable upward bias in the estimates of both the general and specific combining ability variances, whereas its exclusion (Method 3) from the analysis resulted in similar GCA:SCA ratios in all the environments. This investigation supports the exclusion of the parental generation in combining ability analyses. The proportion of general combining ability variance was much higher than that of the specific combining ability variance although both were statistically significant. The interaction of the former with environment was much higher than that of the latter. Except for combining ability variances, the estimates of GCA and SCA effects were found to be alike in both Method 1 and Method 3. Mean performance was correlated with the general combining ability effects. Variety Cb 824 proved to be the best general combiner for earliness; it could be usefully exploited in future breeding programmes to induce earliness, as this variety possesses mostly dominant genes for earliness. Early varieties such as Otis, Bonus M-12a and Line 7-2 were also good combiners for earliness. Crosses between these varieties generally showed high specific combining ability effects.

Introduction

The importance of the concept of combining ability has been widely appreciated both in plant and animal breeding. The concept is especially significant in a breeding programme where it is desired to use genotypes which would combine well in hybrid combinations. A detailed account of combining ability in relation to diallel crossing systems was given by Griffing (1956). Eight different analyses, resulting from a consideration of four different diallel crossing systems together with two alternative assumptions with regard to the sampling nature of the experimental material, were presented and discussed. He suggested that when information on general and specific combining ability for a specific set of lines as well as for a random set of lines is desired in connection with a plant or animal breeding problem, experimental methods 3 and 4 are most suitable. In these methods, parental lines are not included. However, it is evident from the literature that in various crop plants, especially cereals, methods 1 and 2 have invariably been used, requiring the inclusion of parental lines for the analysis. To what extent the inclusion of parents would really bias the estimates of combining ability variances as well as effects is not clearly known and obviously merits study. The present investigation was undertaken to study some of these aspects, using data on the rate of ear emergence in spring barley collected from eight different environments.

Materials and Methods

Ten genotypes of barley were selected on the basis of differences in earliness and diversity of origin. They were: Rika, Proctor, Line 7-2, Line 21-2, No. 191, Abed 894, Otis C.I. 17557, C.I. 1236, Bonus M-12a and Bonus. These were crossed in a diallel fashion and the F_1s and their reciprocals were produced by hand pollination in the glasshouse.

The complete diallel set was grown in eight different environments, the details of which are given in the following table:

Environment	Conditions	Mean date of germination
I	Glasshouse – Gradually increasing daylength and temperature	5. 3. 65
II	Glasshouse – Gradually increasing daylength and temperature higher than I	29. 4. 65
III	Glasshouse – Gradually decreasing daylength at higher temperature than I and II	10. 6. 65
IV	Field – Gradually increasing daylength and temperature but lower than I, II and III	1. 4. 68
V	Growth room 20 °C, 20-hr. photoperiod	21. 2. 66
VI	Growth room 7 °C., 16-hr. photoperiod*	8. 10. 65
VII	Growth room 20 °C., 16-hr. photoperiod	21. 2. 67
VIII	Growth room 15 °C., 13-hr. photoperiod	21. 2. 67

* Transferred to warm glasshouse on 18. 1. 66 to complete heading.

Table 1. *Mean squares for general and specific combining ability estimated*

Source	Mean Squares d.f.							
			Env. I		Env. II		Env. III	
	M1	M3	M1	M3	M1	M3	M1	M3
General combining ability	9	9	1014.7**	158.2**	1096.7**	183.6**	251.7**	249.6**
Specific combining ability	45	35	1193.2**	5.0**	502.2**	31.0**	656.8**	73.8**
Reciprocal effects	45	45	1.5	1.5	1.7	1.7	2.1	2.1
Error	99	99	1.9	1.9	2.2	2.2	5.6	5.6
G. C.A:S.C.A.			1:1.17	1:0.03	1:0.46	1:0.17	1:2.61	1:0.29

** $P < 0.01$

Other relevant details of materials and planting have already been given by Paroda and Hayes (1971). The data was subjected to Griffing's (1956) analyses, and combining ability variances as well as effects were estimated using both the method 1 model I (complete diallel including parents) and method 3, model I (F_1s and reciprocals excluding parents). The mixed model B, which on the face of it is the most suitable for the present material because parents were deliberately selected, was not used because it is based on certain arbitrary and inconsistent assumptions with regard to the mixed elements. However, according to Griffing (1956), combining ability analyses are essentially the same under both model I and mixed model B except for a certain change in the error mean square. Such a change would hardly affect the estimates of combining ability variances or the GCA:SCA ratio. Combining ability variances and general combining ability effects were estimated over all the environments separately, whereas specific combining ability effects were calculated on the basis of pooled data.

Results and Discussion

The estimates of combining ability variances obtained from both the method 1, model I and method 3, model I are given in table 1. It was interesting that the variances estimated by these two methods differed considerably in magnitude and the relative proportions of general combining ability and specific combining ability variances (GCA:SCA ratio) varied in most of the environments. Method 1, model I led to higher estimates of both the GCA and SCA variances in six of the eight environments studied, whereas method 3, model I indicated a preponderance of GCA variance in all eight environments. Paroda and Hayes (1971) have previously reported partial dominance for rate of ear emergence in most of the environments and thus the preponderance of additive genetic variance was established. It is clearly indicated that the exclusion of the parental generation (method 3) proved to be more useful in obtaining unbiased estimates of combining ability variances. Inclusion of the parental generation seemed to cause upward bias in the estimates of both the general and specific combining ability variances (data in table 1), the bias being greater in the latter case. This clearly confirms the statement of Griffing (1956) that methods 3 and 4, in which parents are excluded, provide unbiased estimates of combining ability variances. We have generally found in the literature that the implication of the parental generation in combining ability studies has not been considered seriously and invariably methods 1 and 2 have been used. Although combining ability variances are not the precise estimates of additive and dominance components of genetic variance, otherwise obtained in the case of D and H_1 components in diallel analysis (Hayman, 1954), as these variances are not independent of non-allelic interactions, yet inclusion of the parental generation in the combining ability analysis appeared to be responsible for biased estimates of these variances. This clearly shows that, in order to have precise and unbiased variance estimates, method 3 should be preferred to method 1.

The significance of both the general and specific combining ability variances in all the environments established the role of both the additive and dominance components in the expression of this trait, although the former was greater than the latter. Mean squares due to reciprocal effects were non-significant in all the environments indicating the absence of reciprocal differences among the hybrids studied. These results are in accordance with those reported earlier by Paroda and Hayes (1971) using the Hayman (1954) approach.

On the basis of pooled analysis, an upward bias in both the combining ability variances was again apparent using method 1, in contrast to the estimates obtained from method 3 where the amount of GCA variance was high (table 2). Significant differences between environments were observed, and both the general and specific combining ability variances were found to be interacting significantly with environment. The amount of interaction was high in the case of general combining ability. Similar results have been reported by Matzinger et al. (1959) for yield in corn, Liang (1967) for yield and other characters in sorghum, Paroda and Joshi (1970) for yield and components of yield in wheat and by Paroda and Hayes (1971) for ear emergence in barley. Except for the report by Rojas and Sprague (1952) in corn, *in eight environments using Method 1, Model I and Method 3, Model I*

Mean Squares									
Env. IV		Env. V		Env. VI		Env. VII		Env. VIII	
M1	M3	M1	M3	M1	M3	M1	M3	M1	M3
177.7**	166.4**	367.1**	309.9**	1148.1**	855.9**	1189.6**	48.2**	1272.2**	1228.7**
1305.0**	62.1**	1003.0**	22.7**	4303.2**	51.4	1200.8**	35.0**	2501.2**	159.6**
1.6	1.6	4.9	4.9	37.3	37.3	3.8	3.8	11.5	11.5
0.9	0.9	3.5	3.5	49.1	49.1	10.5	10.5	14.0	14.0
1:7.34	1:0.37	1:2.73	1:0.07	1:3.75	1:0.06	1:1.00	1:0.73	1:1.97	1:0.14

where the interaction of SCA variance was greater, all other investigations support the high interaction of GCA variance. It could be that the additive component of genetic variance is more sensitive to changes in environmental conditions than is the SCA variance. However, the additive component need not necessarily be considered to be less stable. On the contrary, it has shown better stability than the dominance component (see Paroda and Hayes, 1971). Beil and Atkins (1967) also observed GCA × year × location interaction to be more stable than SCA × year × location interaction in sorghum.

Table 2. *Pooled analysis for general and specific combining ability*

Source	d.f.		Mean squares	
	M1	M3	M1	M3
General combining ability	9	9	479.86**	446.03**
Specific combining ability	45	35	12628.11**	426.34**
Reciprocal effects	45	45	1.53	1.53
Environment	7	7	82291.81**	63027.62**
General combining ability × environment	63	63	6037.94**	2654.47**
Specific combining ability × environment	315	245	187.29**	13.26**
Reciprocal effects × environment	315	315	61.87**	61.87**
Error	792	718	10.9	10.9
G.C.A.:S.C.A.	–	–	1:26.1	1:0.95

** $P < 0.01$

On the basis of GCA effects (table 3), it became evident that varieties Otis and Line 7-2 were the best combiners for earliness. Cb 824, which otherwise represented the late group, showed good general combining ability for earliness; almost all the F_1s using this parent were quite early compared with the F_1s involving Otis as well as Line 7-2, in spite of the fact that these varieties were earlier, by almost 15 days, than Cb 824. This indicates that although mean performance has shown good correlation with the GCA effects in most of the environments studied, it is not necessarily true that only early parents would be good general combiners for earliness. This is further substantiated by the fact that Bonus M-12a, the earliest parent in the present material, did not transmit earliness to the F_1s in spite of its negative GCA effects in all the environments. This is mainly because earliness in Bonus M-12a is governed by mostly recessive genes, whereas dominant genes are responsible for earliness in Otis, Line 7-2 and Cb824 (see Paroda and Hayes, 1971). It is evident that even medium to late flowering parents could produce early F_1s and, therefore, one has to be quite critical when selecting good combiners. The mean performance of the parents, which has shown good correlation with GCA effects in this investigation, may sometimes prove to be of limited value, as indicated above, and a generalisation is obviously not possible. Singh and Gupta (1970) also observed that *per se* performance of the parents was not usually associated with their combining ability effects in cotton. Proctor, Line 21-2, Cb 883, Bonus and Rika were quite late flowering and they all exhibited poor combining ability for earlines. The usefulness of these varieties in breeding for earliness in spring barley is, therefore, quite limited, whereas varieties like Cb 824 and Otis might well be exploited.

Considering the GCA effects obtained from Method 1 and Method 3, it appeared that both methods gave a similar picture, as the correlation coefficient between the GCA effects obtained from both the methods was highly significant in all the environments studied. Evidently, any of these methods could be used for finding out GCA effects. This is quite contrary to what was observed in the case of combining ability variances. High correlation was noticed between the GCA effects and the parental mean values in all the environments, revealing a general trend that early parents were mostly good general combiners for earliness, whereas late flowering parents were, in general, poor combiners.

Mean performance of F_1s and the estimates of SCA effects obtained over pooled data, by using both the

Table 3. *Estimates of general combining ability effects obtained in eight different environments using both the Method 1, Model I and the Method 3, Model I (Parental mean values are given in parentheses)*

Variety	Env. I			Env. II			Env. III			Env. IV			Env. V		
	M1		M3	M1		M3	M1		M3	M1		M3	M1		M3
1. Rika	+1.62	(79.0)	+1.86	+1.63	(57.5)	+1.85	+0.59	(52.0)	+6.06	+1.77	(79.9)	+1.99	+1.47	(58.5)	+2.33
2. Proctor	+4.92	(87.0)	+4.99	+4.96	(63.0)	+5.32	+6.44	(61.0)	+6.79	+3.80	(85.0)	+3.88	+3.30	(59.0)	+4.55
3. Line 7-2	−3.45	(70.0)	−3.55	+0.26	(49.0)	−3.55	−5.23	(40.5)	−5.23	−3.85	(69.4)	−2.47	−2.15	(50.0)	−1.13
4. Line 21-2	+2.67	(81.0)	+2.36	+2.31	(60.5)	+2.32	+2.59	(55.5)	+2.66	+3.40	(79.9)	+4.25	+7.32	(79.5)	+7.03
5. Cb 824	−2.95	(84.5)	−4.54	−4.67	(50.5)	−5.42	−2.78	(61.0)	−4.73	−2.48	(84.5)	−3.90	−2.35	(64.0)	−3.13
6. Cb 883	+2.52	(82.5)	+2.55	+2.21	(60.5)	+2.20	+2.94	(57.0)	+2.92	+2.27	(81.1)	+2.46	+3.67	(59.5)	+4.96
7. Otis	−2.85	(73.5)	−3.43	−2.94	(55.5)	−3.61	−4.96	(39.5)	−4.77	−4.26	(72.0)	−4.56	−5.28	(48.0)	−4.79
8. C.I. 1236	+0.77	(77.5)	−2.13	−0.77	(56.5)	−1.18	−0.16	(50.0)	−0.81	−1.65	(78.6)	−2.11	−4.70	(49.0)	−4.19
9. Bonus M-12a	−1.73	(63.0)	−3.25	−1.07	(48.0)	−3.31	−1.53	(39.5)	−0.48	−0.80	(70.5)	−1.20	−4.09	(48.0)	−3.31
10. Bonus	+1.40	(78.5)	+1.64	+2.08	(59.0)	+2.23	+1.97	(52.0)	+2.32	+1.79	(80.1)	+1.98	+2.85	(59.5)	+3.93
C.D. (g_i-g_j) at 5%	1.11		1.11	1.19		1.19	1.91		1.91	0.77		0.77	1.51		1.51
r (between $\bar{x}$ and g.c.a. effects)	+0.71*		+0.59	+0.73*		+0.89**	+0.70*		+0.52	+0.66*		+0.49	+0.82**		+0.73*

Variety	Env. VI			Env. VII			Env. VIII			Mean		
	M1		M3	M1		M3	M1		M3	M1		M3
1. Rika	+ 5.99	(144.0)	+ 5.68	+1.79	(67.0)	+ 5.68	+ 1.79	(116.0)	+ 2.51	+2.24	(81.7)	+3.22
2. Proctor	+10.49	(184.5)	+ 7.09	+9.44	(70.0)	+11.95	+ 9.73	(115.0)	+ 9.15	+5.44	(90.5)	+8.32
3. Line 7-2	− 2.31	(137.0)	− 2.98	−8.09	(54.0)	− 8.52	− 4.22	(88.0)	− 3.60	−3.25	(69.7)	−5.13
4. Line 21-2	+ 5.94	(143.0)	+ 6.92	+9.01	(106.0)	+ 6.67	+11.23	(112.5)	+12.58	+4.42	(89.7)	+6.95
5. Cb 824	− 8.11	(131.0)	− 9.48	−3.46	(92.0)	− 7.18	− 5.02	(111.0)	− 7.54	−4.80	(84.9)	−5.18
6. Cb 883	+ 6.04	(138.5)	+ 8.28	+9.14	(68.5)	+11.51	+ 8.63	(110.0)	+ 9.52	+4.39	(82.3)	+5.98
7. Otis	− 8.26	(114.0)	− 8.10	−8.64	(51.5)	−16.21	− 7.25	(92.5)	− 7.97	−4.68	(68.3)	−7.09
8. C.I. 1236	− 1.21	(132.5)	− 1.38	−8.31	(59.0)	− 9.50	− 8.15	(92.0)	− 9.19	−3.08	(74.5)	−4.26
9. Bonus M-12a	−11.81	(101.5)	−10.42	−4.36	(50.5)	− 31.2	− 9.72	(56.5)	− 6.57	−2.78	(59.7)	−5.69
10. Bonus	+ 4.74	(136.5)	+ 5.34	+4.40	(74.0)	+ 4.98	− 0.50	(113.5)	− 2.19	+2.03	(81.6)	+2.94
C.D. ($g_i - g_j$) at 5%	5.69		5.69	2.62		2.62	3.02		3.02	2.66		2.66
r (between $\bar{x}$ and g.c.a. effects)	+0.84**		+ 0.72*	+0.59		+ 0.42	+ 0.70*		+ 0.56	+0.69*		+0.79**

* $P < 0.05$ ** $P < 0.01$

Table 4. *Mean performance of F_1s (parentheses) and the estimates of specific combining ability effects obtained over pooled data by using both Method 1, Model I (upper diagonal) and Method 3, Model I (lower diagonal)*

Parents	Rika	Proctor	Line 7-2	Line 21-2	Cb 824	Cb 883	Otis	C.I. 1236	Bonus M-12a	Bonus
Rika		1.19 (85.89)	−1.98 (72.61)	−3.66 (80.15)	−3.15 (71.30)	−3.27 (86.09)	−4.37 (68.56)	0.47 (77.55)	6.11 (79.90)	1.00 (81.17)
Proctor	1.11		−0.87 (76.67)	1.06 (88.50)	−3.73 (74.49)	−0.06 (85.95)	0.17 (76.79)	−1.21 (77.92)	3.38 (81.32)	−0.33 (84.45)
Line 7-2	−0.46	−0.78		4.88 (76.49)	−2.32 (65.26)	1.40 (77.60)	−0.68 (66.51)	2.60 (70.84)	−0.85 (66.62)	−0.52 (173.49)
Line 21-2	−3.56	1.21	0.14		1.88 (75.30)	0.49 (86.05)	2.30 (76.35)	−0.01 (77.56)	0.93 (77.49)	−1.58 (81.82)
Cb 824	−1.21	−1.21	−0.24	0.29		−3.46 (72.77)	6.75 (72.69)	−2.21 (66.46)	−7.21 (60.59)	−0.28 (73.69)
Cb 883	2.63	−1.62	0.92	0.10	−0.02		−1.12 (73.71)	−2.34 (74.79)	2.76 (78.79)	2.56 (85.69)
Otis	−4.14	0.46	0.72	2.78	9.07	−1.38		−1.92 (65.04)	−2.78 (62.90)	−3.24 (69.39)
C.I. 1236	1.06	−0.64	3.27	0.73	0.37	−2.32	−1.04		1.31 (69.44)	−2.51 (72.07)
Bonus M-12a	4.98	3.33	−2.83	0.06	−6.26	1.16	−3.52	0.83		3.24 (76.92)
Bonus	0.88	−0.37	−1.72	−1.35	1.68	2.00	−3.03	−2.00	2.15	

r (between *SCA* effects estimated by Method 1, Model I and Method 3, Model I) = 0.88 ($P < 0.01$)

Method 1, Model I, and Method 3, Model I, are presented in table 4. SCA effects obtained from both the methods showed a highly significant correlation coefficient ($r = 0.882$; P 0.01). Inclusion or exclusion of the parental generation had, therefore, no significant effect on the estimates of SCA effects. Thus, either method could conveniently be used for the combining ability effects, but, as the parental generation seemed to bias the combining ability variances, it would be preferable to use Method 3. Considering the SCA effects of individual crosses, crosses Cb 824 × Bonus M-12a and Otis × Bonus M-12a were the best, because both the parents involved were good general combiners for earliness, the F_1s were quite early and they also exhibited high SCA effects. Otis × CI 1236 was also a fairly good cross based on these considerations. Only one cross, i.e. Rika × Otis, which involved one poor combining and late parent and one early and good combining parent, showed high SCA effects and the F_1 was later in flowering by almost 8 days than the earliest F_1, i.e. Cb 824 × Bonus M-12a. Considering the preponderance of additive genetic variance for rate of ear emergence, the general combining ability of parents and the specific combining ability of the early F_1s, it would be most desirable to exploit crosses like Cb 824 × Bonus M-12a, Otis × Bonus M-12a and Otis × CI1236 in breeding spring barley for earliness. Intermating in the segregating generations of these crosses would lead to further accumulation of additive genes for earliness. This could also be achieved by building a population through simple recurrent selection and also by adopting a biparental cross approach in the subsequent segregating generations.

Literature

Beil, G. M., Atkins, R. E.: Estimates of general and specific combining ability in F_1 hybrids for grain yield and its components in grain sorghum, *Sorghum vulgare* Pers. Crop Sci. **7**, 225–228 (1967).

Griffing, B.: Concept of general and specific combining ability in relation to diallel crossing system. Australian J. biol. Sci. **9**, 463–493 (1956).

Hayman, B. I.: The theory and analysis of diallel crosses. Genetics **39**, 789–809 (1954).

Liang, G. H.: Diallel analysis of agronomic characters in grain sorghum, *Sorghum vulgare* Pers. Canad. J. Genet. Cytol. **9**, 269–276 (1967).

Matzinger, D. F., Sprague, G. F., Cockerham, C. C.: Diallel crosses of maize in experiments repeated over locations and years Agron. J. **51**, 346–350 (1959).

Paroda, R. S., Joshi, A. B.: Genetic architecture of yield and components of yield in wheat. Indian J. Genet. **30**, 298–314 (1970).

Paroda, R. S., Hayes, J. D.: An investigation of genotype-environment interactions for rate of ear emergence in spring barley. Heredity **26**(2), 157–176 (1971).

Rojas, B. A., Sprague, G. F.: A comparison of variance components in corn yield trials. III. General and specific combining ability and their interactions with locations and years. Agron. J., **44**, 462–466 (1952).

Singh, R. B., Gupta, M. P.: Combining ability for yield characters in upland cotton. Indian J. Genet. **30**, 608–618 (1970).

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