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Combining Ability and Heterosis in Diallel Crosses of Maize*

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Summary. The present investigation involved crosses among 20 elite yellow maize populations. These were evaluated in four environments in a randomized block design with four replications in each environment. Variety Cuba was observed to be the best general combiner for grain yield, followed by St Croix and Prolific. No clear association could be discerned between general combining ability (GCA) effects for grain yield and its components, and mean grain yield performance and GCA effects. Heterosis was observed in general and all the crosses involving Cuba yielded better than the midparent. The five hybrids, Kisan × Cuba, Antigua 3D × St Croix, Prolific × St Croix, Vijay × Antigua Gr.I and A 23 × Cuba, yielded more than the standard check. Significant yield superiority of these varietal hybrids over the best commercial composite (Jawahar) suggested the possibility of their commercial exploitation.

Introduction

Because of the lack of proper understanding of gene action involved in the expression of heterosis, commercial use of varietal crosses has not received due attention in the past, even though Beal (1878) reported heterosis to the extent of 40 per cent over the better parent. In recent studies on maize, additive genetic variance has been shown to predominate in open pollinated varieties, in the expression of yield and other metric traits (Gardner 1963; Gardner and Lonnquist 1966), and successfully exploited by employing intrapopulation selection schemes (Gardner 1969).

These studies have suggested the possibility of synthesizing broadbased composite population or gene pools, comparable in yield to commercial hybrids. Moreover, such populations would be amenable to further selection. Promising composites can be combined in varietal hybrids, which are better suited to developing countries due to convenient seed production. For formulating an effective programme to breed composite varieties and their hybrids, a knowledge of the combining ability of the materials being handled is essential. The present study was undertaken along these lines.

Materials and Methods

Crosses among 20 yellow maize populations, eleven developed in India and nine obtained from Mexico, formed the material. The parental populations were selected primarily on the basis of their own performance as well as of hybrids involving them. The populations developed in India were five commercial composites (Amber, Jawahar, Kisan, Vijay and Vikram), three experimental composites (C 2, J 236 and Prolific) and three experimental synthetics (A 22, A 23 and E 13), while the populations obtained from CIMMYT, Mexico, were four composites (Antigua Group 1, Caribbean Flint, Puerto Rico Group 1 and Yellow Tuxpeno) and five open pollinated varieties (Antigua 2D, Antigua 3D, Cuba 19, St Croix 4D and Francisco Flint). All possible crosses were made and bulked seed of crosses and reciprocals was laid out in a randomized block design with four replications during the rainy seasons of 1970 and 1971 at the Indian Agricultural Research Institute, New Delhi, and Gobind Ballabh Pant University of Agriculture and Technology, Pantnagar. These locations represented Indo-Gangetic plains and sub-montaneous *Kamaon* foot hills region, respectively. The two years and two locations were assumed to represent four random environments.

Grain yield per plant and days to silk were based on whole plot observation. Plant height, ear height, ear length, ear diameter and number of kernel rows were recorded on 10 randomly selected plants and their means were used for analysis. At harvest, fresh ear weight was recorded for each plot and was adjusted to 15 per cent grain moisture and 80 per cent shelling.

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Table 1. Analysis of variance for combining ability

Source	d.f.	Mean squares							
		Grain yield	Days to silk	Grain moisture	Plant height	Ear height	Ear length	Ear diameter × 10	Kernel rows
GCA	19	3570.9**	178.0**	77.0**	13957.9**	8536.4**	23.6**	18.8**	44.6**
SCA	170	639.0**	11.0**	6.0*	400.8**	272.2**	3.2**	0.8**	1.6**
GCA × E	57	1461.4**	19.2**	15.5**	328.2**	339.7**	3.2**	1.2**	0.9**
SCA × E	510	478.2**	7.4**	5.4	202.5**	113.9**	1.6	0.5**	0.5
Pooled error	2268	315.0	5.7	5.0	173.7	96.4	1.6	0.4	0.5

*, ** Significant at 5 per cent and 1 per cent level, respectively

Days to silk were recorded as days taken to silk emergence of 75 per cent of plants in a plot. Moisture percentage was determined using the 'Universal Moisture Tester' in a grain sample obtained from two rows of each of the five ears selected at random at the time of harvest.

Combining ability analysis was based on the procedures developed by Singh (1973). Method 4 was employed assuming the fixed effects (Model I).

Results and Discussion

Analysis of variance showed significant differences among hybrids. The combining ability analysis (Table 1) suggested the presence of significant variation due to general (GCA) and specific combining ability (SCA) for all characters. It was also true for GCA × E interaction while SCA × E was significant for grain yield, days to silk, plant height, ear height and ear diameter only. Variation accounted for by combining ability effects, in general, was appreciably higher in comparison with interaction effects of GCA and SCA with environments.

Only three varieties, Cuba, St Croix and Prolific, had a GCA effect significantly greater than zero for grain yield (Table 2). Cuba had distinctly higher GCA effects than the others. These three parents were good general combiners for one or more yield components. However, any clear association between yield and its components was lacking, though Cuba was a good combiner for ear length, St Croix for ear

Table 2. Estimates of general combining ability effects

Code	Pedigree	Grain yield	Days to silk	Grain mois-	Plant height	Ear height	Ear length	Ear diameter × 10	Kernel rows
1	Amber	-0.4	1.1*	0.2	5.7*	1.8*	0.3*	0.1	0.0
2	Jawahar	-3.9*	0.3*	-0.3*	-1.9*	-1.6*	0.2*	0.0	0.4*
3	Kisan	-1.4	0.3*	0.2	-1.7*	0.3	0.2*	-0.1	-0.1
4	Vijay	0.8	0.0	-0.1	3.3*	1.9*	0.1	0.1	0.3*
5	Vikram	-3.0*	-0.3*	0.2	-0.6	0.0	0.3*	-0.6*	-0.4*
6	C 2	-2.0	-0.8*	-1.0*	-7.2*	-8.4*	0.1	-0.2*	0.0
7	J 236	0.3	0.3*	-0.1	2.7*	1.5*	0.0	-0.1	0.0
8	Prolific	4.8*	-1.1*	-0.9*	5.7*	0.7	-0.4*	-1.1*	0.1*
9	A 22	-1.3	-0.5*	0.1	-0.1	1.4*	0.0	0.0	0.0
10	A 23	1.1	0.0	0.2	-4.9*	-0.9	-0.6*	1.0*	0.1*
11	E 13	-2.7*	-0.9*	-0.3*	-1.9*	-2.2*	-0.2*	0.1	0.1*
12	Antigua Gr.1	1.1	-1.2*	-0.4*	-15.0*	-9.4*	-0.4*	1.0*	0.7*
13	Antigua 2D	1.7	-0.4*	0.0	-15.0*	-10.6*	-0.2*	0.8*	0.5*
14	Antigua 3D	-1.4	0.3	0.0	1.1	1.5*	0.0	0.0	0.1*
15	Caribbean Flint	-2.0*	1.2*	-0.3*	6.1*	5.4*	0.1	-0.7*	0.0
16	Cuba	10.6*	1.0*	1.4*	6.7*	3.3*	0.7*	0.0	-0.8*
17	Puerto Rico Gr.I	-2.0*	-1.2*	-0.3*	-2.5*	-0.2	0.2*	-1.6*	-0.5*
18	St Croix	5.1*	0.1	0.2	2.8*	-1.4*	0.0	2.1*	0.2*
19	Yellow Tuxpeno	-1.6	1.2*	0.5*	13.9*	14.9*	-0.3*	-1.0*	-0.8*
20	Francisco Flint	-3.9*	0.6*	0.7*	2.9*	2.0*	-0.1	0.1	0.0
S.E. ($\hat{g}_i$) ±		1.02	0.14	0.12	0.76	0.56	0.07	0.12	0.04

* Significant at 5 per cent level

diameter and kernel rows, and Prolific for kernel rows. Of the six poor combiners for grain yield (Francisco Flint, Jawahar, Vikram, E 13, Caribbean Flint and Puerto Rico Gr.1), four were good combiners for one or other yield component, supporting the above observation.

There was an indication that the yield superiority of Cuba, and to a lesser extent of St Croix, was due to late maturity. Similar results were also recorded in six diallel crosses, comprising varieties of varying maturity range, studied by the All India Coordinated Maize Improvement Scheme (Progress Report 1972). Accordingly, there is a need for greater care to record grain yield unbiased for maturity, to obtain estimates of GCA relevant to practical breeding. Two approaches are possible: (i) to study grain yield per day; and (ii) to adjust yield for average maturity through regression technique. The second approach is being applied to host-pest resistance studies in the European corn-borer, particularly in correcting relative oviposition for plant height. Further work on these lines is desirable.

Dhillon et al. (1977) reported mean performance of these parental populations. Cuba was distinctly different from the other materials, being the poorest yielder, having the longest, thinnest cobs and taking maximum days to silk. In combining ability analysis, it had the highest GCA effect for grain yield and ear length, indicating complete agreement between mean performance and GCA effect for ear length but exactly the reverse for grain yield. Another divergent parent was Antigua 2D, which had the shortest plants, lowest ear placement and maximum number of kernel rows. It was also the best combiner for short plant type and second best for kernel rows. St Croix, an above average yielder, had the thickest ears and was also the best general combiner for ear diameter. Antigua 3D, Jawahar and A 22 were better yielders and average

Table 3. Estimates of specific combining ability effects of some hybrid

Pedigree[a]	Grain yield	Days to silk	Grain moisture	Plant height	Ear height	Ear length	Ear diameter	Kernel rows
Good Specific Combiner For Grain Yield								
1 × 17	17.1*	-1.8*	-0.4	0.4	-1.8	1.1*	-0.4	-0.4*
1 × 20	11.1*	0.8	0.5	4.4	0.7	0.5	0.9	0.5*
2 × 15	10.1*	-1.2*	0.4	3.1	0.0	0.3	-0.1	-0.2
3 × 16	13.6*	0.4	-0.5	-0.2	-0.2	0.4	0.3	0.0
4 × 12	13.4*	0.0	0.1	-1.9	-3.1	0.1	0.1	-0.3
4 × 18	9.2*	-0.5	0.8	6.2*	5.0*	0.3	1.7*	-0.3
6 × 10	12.6*	0.0	-0.2	3.6	0.5	-0.2	-0.3	-0.5*
6 × 13	10.0*	-0.7	-0.2	7.4*	7.0*	0.4	0.4	0.2
8 × 20	14.1*	-1.3*	0.8	3.0	6.0*	-0.3	0.1	0.3
9 × 15	9.1*	-1.0	1.2*	0.1	1.4	0.2	1.9*	0.1
11 × 15	11.2*	0.1	-0.3	0.2	0.2	-0.1	-0.6	-0.1
12 × 19	13.9*	-0.5	0.7	1.4	-2.4	0.4	0.4	-0.2
14 × 18	16.6*	-0.8	0.8	9.2*	1.7	0.4	0.4	0.2
Poor Specific Combiner For Grain Yield								
2 × 3	-8.5*	-1.1	0.2	3.4	-1.2	0.8*	0.7	0.0
2 × 8	-10.7*	0.9	0.4	8.1*	4.9*	0.5	-1.1*	-0.6*
3 × 9	-8.5*	1.0	0.1	-0.7	-2.0	-0.1	-0.4	-0.6*
4 × 6	-11.2*	-0.4	0.1	-6.0	-1.3	-0.7*	-0.4	-0.2
4 × 8	-9.3*	0.4	-1.0*	-5.7	-1.5	-0.1	-0.1	0.2
5 × 10	-11.9*	0.0	0.4	-3.6	-1.2	-0.5	-1.1*	-0.2
6 × 8	-17.2*	2.2*	-0.7	-2.1	-0.4	-0.5	-0.2	0.4*
7 × 18	-8.8*	2.0*	-0.7	1.1	2.3	0.0	-1.1*	-0.6*
9 × 19	-10.5*	0.2	-0.4	-0.9	-1.9	0.4	0.2	-0.2
12 × 13	-22.8*	1.7*	-0.7	-13.7*	-7.8*	-1.0*	-2.4*	-0.1
14 × 16	-8.8*	0.6	0.0	-10.5*	-0.8	-0.8*	-1.0*	0.2
14 × 17	-9.2*	-0.3	0.5	4.1	-0.8	-0.5	1.6*	0.5*
15 × 19	-13.9*	0.2	-0.1	-10.4*	-7.5*	-0.9*	-0.6	0.2
17 × 18	-8.9*	1.4	0.4	-12.9*	-10.5*	-0.2	-1.0*	-0.3
S.E. (s_{ij}) ±	4.20	0.56	0.51	3.12	2.32	0.30	0.48	0.17

* Significant at 5 per cent level
[a] Pedigree code is given in Table 2

general combiners, except for Jawahar which was a poor general combiner.

Hybrids with significant positive SCA effects for grain yield were Amber × Puerto Rico Gr.I, Antigua 3D × St Croix, Prolific × Francisco Flint, Antigua Gr.1 × Yellow Tuxpeno, Kisan×Cuba, Vijay × Antigua Gr.1, C 2 × A 23, E 13 × Caribbean Flint, Amber × Francisco Flint, Jawahar × Caribbean Flint, C 2 × Antigua 2D, Vijay × St Croix and A 22 × Caribbean Flint (Table 3). Fifteen hybrids had significant SCA effects for early maturity and, of these, Amber × Puerto Rico Gr.1, Jawahar × Caribbean Flint and Prolific × Francisco Flint combined desirable effects for both yield and maturity. None of the hybrids with positive SCA for yield showed significant SCA effects either for short stature or for low ear placement. However, the three hybrids cited above were medium combiners for ear placement (except Prolific × Francisco Flint) and plant height. Fourteen hybrids had significant negative SCA effects for grain yield and these were, in general, associated with positive SCA effects for silking and negative SCA effects for height and ear characters.

Amber × Puerto Rico Gr.I, Jawahar × Prolific, Vijay × St Croix, C 2 × Antigua Gr.1, J 236 × St Croix, A 22 × Antigua 3D, E 13 × Francisco Flint, Antigua Gr.I × Antigua 2D, Antigua 3D × Cuba, Caribbean Flint × Yellow Tuxpeno, Cuba × Puerto Rico Gr.I, Puerto Rico Gr.I × St Croix and St Croix × Yellow Tuxpeno showed significant SCA effects for four or more traits. Of particular interest was the hybrid Antigua Gr.1 × Antigua 2D, which had the highest number of significant SCA effects (for all traits except grain moisture and kernel rows). It had the lowest SCA effects for grain yield, plant height and ear diameter. Such poor performance was expected, since the parents are close related in origin.

Consideration of GCA effects of the parents involved in the crosses showing significantly positive and negative SCA effects for yield indicated no association between expression of GCA and SCA effects. None of the hybrids showing significantly negative SCA effects was either a poor × poor or a good × good cross; the same was the case for hybrids with significantly positive SCA effects except for two poor × poor combinations (Jawahar × Caribbean Flint and E 13 × Caribbean Flint). A good general combiner (Prolific) was the most common parent amongst the hybrids showing significantly negative SCA effects, while a poor general combiner (Caribbean Flint) was the most common parent in the other group of hybrids. It was also interesting that the hybrid of the best general combiner (Cuba) and best yielder (Antigua 3D) showed significantly negative SCA effects.

Sixty-three hybrids showed significant superioity in grain yield over mid-parent and the maximum heterosis was 40 per cent for Kisan × Cuba (Table 4). It was interesting that all the crosses involving Cuba yielded better than the mid-parent with a range of 6 to 40 per cent. Cuba was also involved in six of the top eight hybrids. The performance of Cuba, and its practical implications, have been discussed by Dhillon and Singh (1975). Prolific, also a good combiner like Cuba, was the second most common parent, but St Croix another good general combiner, trailed behind A 23, Antigua Gr.1, Antigua 2D, Yellow Tuxpeno and C 2. Significant heterosis over better parent was obtained for 32 hybrids. Three hybrids (Kisan × Cuba, C 2 × Cuba and A 23 × Cuba) showed one-third greater yield than the better parent.

Eighteen hybrids were highly heterotic, as they performed significantly better than mid-parent for four or more characters (Table 4). Heterotic responses of various traits exhibited a definite association between them in these hybrids. Grain yield was associated with yield components, particularly ear diameter and kernel rows. Contrary to previous indications, these hybrids combined heterotic responses for high yield and early maturity. None of these hybrids was heterotic for lower ear placement (except Antigua Gr 1 × Caribbean Flint) and short plant height. The best general combiner (Cuba) was a parent of 50 per cent of the highly heterotic combinations. This was expected as Cuba was the most diverse parent. The second most common parent was St Croix (good general combiner for yield) and it was involved in five hybrids. With regard to the contribution of highly heterotic hybrids, the third good general combiner for yield (Prolific) was overtaken by Antigua Gr.I, Vijay, Caribbean Flint and Francisco Flint.

In a practical breeding programme, it would be useful to test the superiority of a hybrid over a standard cultivar. In the present study, Jawahar was the highest-yielding standard cultivar and only five hy-

Table 4. Performance of some promising hybrids as per cent of mid-(MP) and better-parent (BP)

Heterotic Hybrids For Grain Yield

Pedigree[a]	MP	BP	Pedigree	MP	BP	Pedigree	MP	BP
1 × 10	115*	111	5 × 16	122*	117*	9 × 16	119*	108
1 × 12	117*	113*	6 × 10	129*	127*	10 × 12	116*	116*
1 × 16	120*	113*	6 × 12	122*	120*	10 × 13	112*	110
1 × 17	118*	116*	6 × 13	125*	121*	10 × 16	134*	131*
1 × 20	116*	113*	6 × 16	133*	132*	10 × 17	113*	107
2 × 16	120*	108	6 × 19	114*	112	10 × 19	112*	112
3 × 6	116*	112	6 × 20	114*	110	11 × 16	121*	113*
3 × 8	113*	112	7 × 8	116*	111	12 × 16	128*	125*
3 × 10	112*	111	7 × 12	113*	105	12 × 19	128*	128*
3 × 12	111*	109	7 × 13	115*	105	12 × 20	115*	113*
3 × 16	140*	135*	7 × 16	115*	109	13 × 16	126*	121*
3 × 19	113*	112	8 × 9	111*	105	13 × 18	112*	107
4 × 10	113*	106	8 × 10	124*	121*	13 × 19	112*	111
4 × 12	122*	114*	8 × 12	118*	115*	14 × 18	116*	113*
4 × 13	114*	108	8 × 13	119*	117*	15 × 16	112*	104
4 × 16	119*	110	8 × 15	114*	110	15 × 18	111*	110
4 × 18	115*	114*	8 × 16	128*	122*	16 × 17	118*	110
4 × 19	113*	106	8 × 17	112*	108	16 × 18	125*	115*
5 × 6	112*	107	8 × 18	120*	116*	16 × 19	128*	125*
5 × 8	116*	116*	8 × 19	118*	116*	16 × 20	123*	118*
5 × 13	115*	114*	8 × 20	125*	124*	18 × 19	111*	105

Highly Heterotic Hybrids (MP)

Pedigree[a]	Grain yield	Days to silk	Grain moisture	Plant height	Ear height	Ear length	Ear diameter	Kernel rows
1 × 16	120*	96*	96	105	106	102	105*	104*
2 × 16	120*	97*	98	103	102	99	106*	104*
3 × 16	140*	95*	93*	106	107	102	107*	104*
4 × 13	114*	96*	102	106	104	104	105*	106*
4 × 15	101	96*	91*	99	96	99	104*	107*
4 × 16	119*	96*	99	111	106	102	106*	105*
5 × 16	122*	96*	92*	106	109	102	106*	106*
7 × 12	113*	96*	97	99	98	107*	106*	104*
8 × 18	120*	97*	104	106	110	102	104*	105*
10 × 16	134*	97*	99	106	108	105*	110*	104*
12 × 15	100	97*	95	97	95*	103	106*	107*
12 × 16	128*	94*	98	102	97	100	108*	109*
12 × 20	115*	95*	97	104	108	102	105*	106*
14 × 18	116*	98*	103	108	107	101	103*	104*
15 × 18	111*	96*	98	108	110	101	104*	106*
16 × 18	125*	94*	93*	113	113	104	106*	109*
16 × 20	123*	94*	94*	106	105	96	105*	102
18 × 19	111*	97*	97	106	107	97	105*	106*

* The differences between hybrid mean and parent mean significant at 5 per cent
[a] Pedigree code is given in Table 2

brids (Kisan × Cuba, Antigua 3D × St Croix, Prolific × St Croix, Vijay × Antigua Gr.1 and A 23 × Cuba) yielded significantly better than Jawahar (the superiority being 11 to 18 per cent). Extensive evaluation of these five varietal hybrids would be desirable for commercial exploitation. Varietal hybrids have the edge over the standard inbred-hybrid approach in convenient seed production. Because of the broad genetic base, such hybrids are also expected to be more stable in their performance in the face of weather fluctuations and pests and diseases. They are also amenable to further improvement by selection. It is worthwhile adding that varietal hybrids are being commercially grown and further improved in Kenya (Darrah et al. 1972).

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