Inter-character Relationships and Heterosis Observed in Opaque-2 Maize Crosses and in their Normal Analogues

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Summary. Hybrids obtained from two series of diallel crosses made between six o_2 converted inbred lines on the one hand and their normal analogues on the other were compared for twenty-five characters including yield and several of the yield components, including the parents. Observations on simple inter-character correlation coefficients presented here have shown that the majority of the correlations at the o_2 level are of the same order as at the normal level. A number of correlations of the o_2 type are inferior to those of their normal analogues, whereas a few are favoured by the o_2 gene including the correlation of grain yield with kernels per row. A measure of heterosis for each hybrid over its mid-parent also demonstrated that the o_2 types show poorer heterosis in more cases than do their normal counterparts. Still, in nearly 40 percent of the cases the o_2 hybrids were found to be more heterotic than their normal analogues, particularly for the various maturity characters and several of the yield components. Thus, the possibility of improvement exists in breeding maize with the opaque-2 gene.

Utilization of the o_2 recessive endosperm mutant gene, isolated by Singleton and Jones (Emerson *et al.*, 1935), in the large scale commercial production of high quality Zea mays L. is as yet unrealized. The o_2 hybrids were found to be generally lower in yield, kernel weight and kernel density, and higher in grain moisture at harvest than their normal counterparts (Lambert *et al.*, 1969; Alexander *et al.*, 1969; Feist and Lambert, 1970). The present study was undertaken to examine the interrelationships among a number of plant characters as well as heterosis for these characters, including yield and several of the yield components, particularly the kernel characteristics, in opaque-2 and normal analogous diallel crosses of six inbred lines of maize.

Materials and Methods

The experiment comprises the same materials and methods reported earlier (Gupta and Kovács, 1974a and b). In addition, observations were also made on all the plants as to height, ear placement, tillers, number of ears, raw ear yield, shelling percentage, grain yield expressed at 15 percent moisture level, ear length, ear diameter, kernel rows, kernels per row, kernels per ear calculated as the product of kernel rows and kernels per row, rachis weight and rachis diameter in the trial conducted during 1972 at Martonvásár.

A correlation coefficient for each character with all the rest was calculated as per Snedecor (1956) for the opaque-2 and the normal types individually, using the averages of each genotype (6 parents and the 15 single cross hybrids in each type, o_2 and normal) over the replications and population density levels of 40,000 and 80,000 plants per hectare.

Average heterosis was calculated for each of the opaque-2 single cross hybrids and their analogous normal crosses as the increase expressed as a percentage of their mid-parent (average of the two parents) values, and their significance was tested using the Student's *t*-test (Fisher, 1926).

Results

Analysis of variance of observations on some of the characters, including the yield and various yield

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Source	df	Plant height	Ear height	Tillers	Number of cars	Raw ear yield	Shelling %-age
Replications Genotypes Error (a)	2 20 40	826.3** 12767.2** 130.9	164.4 4183.6** 59.9	0.283 1.677 0.913	0.074 0.642 0.465	3166.9 94382.7 ** 2993.3	103.5* 663.4** 20.8
Opacity Genotypcs × opacity Error (b)	1 20 42	314.6** 429.9** 19.5	3268.8** 393.4** 38.4	1.092** 0.335** 0.071	0.074 * 0.043 ** 0.015	143.3 5526.0** 543.5	23.9 207.2** 56.0
Density Genotypes × density Opacity × density Constitutes × opacity	1 20 1	17.7 101.9 24.2	134.2** 32.1* 6.6	9.404** 0.308** 0.514**	0.415 ** 0.014 0.009	122057.9** 1951.4** 2097.1	0.8 318.0** 36.3
Genotypes × opacity × density Error (c) Total	20 84 251	72.7 80.3	30.0 18.3	0. 239** 0.0 1 0	0.0 29 0.0 1 9	1077.0 * 533.2	76.7 * 44.6

*, ** significant at 5% and 1% levels of significance respectively.

components, is presented in Table 1. The analysis of variance of the characters not included in Table 1 can be found elsewhere (Gupta and Kovács, 1974a and b). It may be pointed out that the analysis shows significant differences among the opaque-2 and the normal analogues for such characters as plant height, ear height, total leaves, leaves above ear, number of tillers, days to 50 percent pollen-shed, days to 50 percent silking, number of ears, ear length and kernel density; the differences are not statistically significant in the case of ear leaf area, raw ear yield, drying percentage of the ear, shelling percentage, grain yield, ear diameter, kernel rows, kernels per row, kernels per ear, rachis weight, rachis diameter, kernel length, kernel width, 1000 grain weight and percentage of water imbibed by kernels in 24 hours. In contrast, the mean squares due to genotypes \times opacity interaction are significant for all these characters except the drving percentage of the ear and the water imbibing capacity of the kernels.

Correlation Coefficients

Simple phenotypic correlation coefficients (r) calculated between various characters at the o_2 and the normal levels are presented in Table 2. All the correlation coefficients are positive in value as expected. The table also includes the correlation coefficients between the performance of a given character at the opaque-2 and the normal levels. It will be seen that the opaque-2 types are highly significantly correlated with the normal types (significant at 1% level) for all the characters, except for leaves per plant and percentage of water imbibed by kernels in 24 hours which showed a r significant only at the 5% level. There are, however, three characters - leaves above ear, drying percentage of the ear and kernel density - which showed a statistically not significant correlation coefficient in this experiment between the o, and the normal types, indicating differences between genotypes. In addition the table includes correlation coefficients between the performance of each character at the two levels of population density, that is, at 40,000 and 80,000 plants per hectare, irrespective of the o_2 or normal phenotype of the kernel. All the correlation coefficients were found to be significant at the 1% level of significance.

Although there appears to be no particular trend towards the o_2 types showing a better inter-character correlation than the normal or vice versa (Table 2), it will be seen that some of the characters provide definite evidence of a poorer correlation with other phenotypic characters at the o_2 level than at the normal level. Thus, the characters of plant height, ear height and water imbibing capacity of the kernels need particular mention: in the majority of the cases, if not consistently, they show a poorer value of r at the o_2 level than at the normal level. The characters, ear leaf area and the days to 50 percent silking, also show a similar trend in their relationships with other characters. On the other hand, a few of the characters demonstrate a better correlation with others at the o_2 level than in their normal counterparts. Particularly noteworthy are kernel density, kernel rows and the number of ears per plant.

Data have also been presented in Table 2 on the significance of differences between the two correlation coefficients calculated for each pair of characters, one at the o_2 level and the other at the normal level. The characters particularly showing significant differences between their values of r with other characters at the two levels of opacity are height of the ear and water imbibing capacity of the kernels. The characters, kernels per row, days to 50 percent silking, grain yield and kernels per ear, also demonstrate a similar trend, if not too frequently. On the other hand, several characters seem to have been unaffected in their relationships with other characters by the incorporation of the o_2 gene. Examples are leaves above ear, ear leaf area, tillers, ears per plant, 1000 grain weight and kernel density. On close examination of the cases in which the values of r have

Grain yield	Ear length	Ear diameter	Kernel rows	Kernels per row	Kernels per ear	Rachis weight	Rachis diameter
4085.6*	4.93	0.153	2.32	14.5	2436.4	88.6	0.036
17370.3**	138.49**	3.667 **	23.77**	755.6**	246698.0**	1205.1**	1.626**
911.3	3.58	0.069	1.95	18.8	6301.6	42.5	0.437
7.2	16.92**	0.045	1.71	10.2	1428.3	54.8	0.002
962.5**	8.21**	0.257 **	5.16**	52.3**	18474.7**	102.0**	1.430**
246.4	1.49	0.081	0.91	12.4	3590.9	18.1	0.040
20983.6**	127.57**	0.991 **	8.48 **	357.6**	155367.2**	1579.8**	0.443 **
555.3**	1.74	0.035	0.37	15.0**	4190.2*	21.6**	0.014
237.2	0.04	0.092	0.47	1.9	826.6	3.5	0.081
479.0 *	1.86	0.045	0.49	12.8**	2721.3	7.7	0.020
247.5	1.21	0.028	0.57	5.4	2404.4	9.7	0.022

observations on few of the characters

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Character	Character		1	2	3	4	5	6	7	8	9	10
O ₂ and normal Dense and norr	nal pop		. 93 . 97	. 81 . . 97	.47 .98	. 32 . 96	. 7 2 . 99	. 67 . 90	. 71 . 98	.85 .99	. 86 . 96	. 80 . 90
1. Plant heigh		o_2 +	• 97	.88	. 31	.46	.87	. 28	. 31	.40	.63	. 84
2. Ear height		+ 02 +		.96	. 32	·35 ·13	.83 .73	, 30 , 10	.68 .00*	.74 .00*	.70 .33	.88 .54*
3. Leaves per	plant	$\stackrel{+}{\overset{o_2}{+}}$. 24	. 20	.78 .09	.33	.66 .50	.67 .41	.71 .30	.86
4. Leaves abo	ve ear	+ 02 +				.63	. 26 . 34	.19	.14 .24	. 25 . 28	.07 .42	.28 .60
5. Ear leaf are	ea	02					. 31	.19 .17	. 30 . 24	.46 .34	. 20 . 58	· 33 · 77
6. Tillers		+ 02 +						.19	.67 .61	.73 .57	· 57 · 53	·79 ·45
7. Days to 50°	% pollen-shed	+ 02 +							.65	. 50 . 96	. 46 . 78	. 55 . 58
8. Days to 50 ⁶	% silking	+ 02 +								. 91	.79 .84	.84 .67
9. Number of	ears	-+ 02 -+									.85	.87 .87
10. Raw ear yi	eld	+ 02 +										. 84
11. Drying %-a	age of ear	+ 02 +										
12. Shelling %-	-age	$\stackrel{+}{\scriptstyle o_2}$										
13. Grain yield		$\stackrel{+}{\overset{0_2}{+}}$										
14. Ear length		+ 02 +										
15. Ear diamet	er	$\stackrel{+}{\overset{o_2}{+}}$										
16. Kernel rows	5	o_2										
17. Kernels per	row	+ 02										
18. Kernels per	ear	+ o_2										
19. Rachis weig	ght	+ 02 +										
20. Rachis dian	neter	+ 02 +										
21. Kernel leng	th	+ 02 +										
22. Kernel widt	h	$\stackrel{+}{\overset{o_2}{+}}$										
23. 1000 grain v	weight	$\stackrel{+}{\scriptstyle -}$										
24. Kernel dens	ity	$\stackrel{+}{\overset{o_2}{+}}$										
	bibed											

Table 2. Intercharacter correlation coefficients at the opaque-2 and the normal levels of opacity

^a Correlation coefficients greater than 0.43 and 0.54 are significant at 5% and 1% levels of significance respectively. Degrees *, ** indicate significance of differences between the analogous correlation coefficients at the o_2 and the normal levels at

and intracharacter correlation coefficients at the two levels of opacity and density, a

1	12	13	14	15	16	17	18	19	20	21	22	23	24	25
28 73	.59 .90	.89 .95	.89 .97	.87 .98	.64 .96	.87 .96	.86 .97	.85 .97	.86 .98	.75 .91	.76 .97	.82 .95	.39 .59	.48 .79
3 4	.38 .56	.70 .85	.87 .94	·77 .80	.42 .25	.82 * .96	.75 .91	.81 .84	.78 .75	.59 .70	.80 .85	. 56 .66	.23 .13	.00 .47
4 7	.00 .52	.37 * .83	.61 ** .96	.46 * .82	.08 .12	.55 ** .96	.44 ** .87	.54 .84	. 54 .81	.27 .64	.58 * .89	.32 .68	.03 .23	.00 .52
6** 0	· .46 .00	.25 .23	.03 .27	.12 .30	.11 .11	.00 .34	.00 .35	.17 .31	.00 .28	.24 .27	.08 .13	.51 .03	.68 .20	.45 .00
4 8	.24 .42	.47 .30	.50 .15	.52 .25	.48 .61	.51 .28	. 56 .46	.56 .17	.51 .09	.45 .49	.36 .04	.14 .00	.05 .12	.00 .24
8 0	.22 .43	.67 .81	.87 .82	.72 .77	.33 .34	.80 .80	.71 .82	.80 .83	.81 .67	.45 .79	.73 .79	.58 .67	.32 .13	.24 .64
6 2	.51 .52	.53 .54	.40 .37	.54 .53	.79 .41	.47 .44	.63 .53	.42 .38	.42 .42	.61 .56	.33 .18	.45 .45	.48 .51	.00 .44
5	.92 * .69	.74 .83	.56 .72	.75 .83	.79 .59	.60 .71	.69 .83	.50 .74	.56 .72	.87 .83	.66 .57	.80 .78	.79 .55	.40 .74
0 0	.95 ** .73	.78 .87	.65 .71	.83 .84	.84 .65	.67 .75	.76 .87	.60 .76	.66 .71	.89 .89	.73 .59	.78 .78	.80 .52	.30 * .77
0	.82 .76	.93 .81	.84 .74	.92 .81	.72 .48	· 57 · 74	.84 .80	.76 .72	.81 .77	.88 .67	.84 .60	.88 .84	.72 .64	.20 .64
0 8	.58 .64	.91 .96	.95 .91	.86 .94	.64 .42	.94 .93	.93 .95	.94 .9 2	.86 .85	.78 .85	.86 .79	.73 .86	.45 .41	.10 * .76
	.44 .34	.14 .15	.16 .18	.00 .32	.16 .24	.10 .17	.07 .24	.20 .10	.13 .37	.23 .18	.00 .04	.30 .25	.51 .33	.43 .26
		.71 .64	.52 .47	.72 .48	.74 .75	-55 -50	.60 .67	.44 .41	.38 .33	.87 .65	.65 .32	.72 .61	.75 .52	.10 .46
			.89 .90	.89 .91	.66 .45	.87 ** .31	.86 .96	.81 .92	.78 .81	.86 .86	.85 .78	.86 .86	.63 .42	.28 * .77
				.92 .87	.60 .12	.96 .96	.92 .89	.94 .93	.91 .86	.74 .67	.89 .93	.76 .78	.47 .28	. 2 0 .60
				·	.77 .36	.90 .87	.91 .89	.87 .90	.94 .96	.88 .84	.87 .78	.80 .84	.58 .40	.30 * .77
					-	.67 .17	.84 .51	.64 .22	.65 * .09	.78 .68	.55 .08	.54 .32	. 59 . 31	.14 .45
							.94 .93	.93 * .70	.88 .83	.74 .72	.87 .88	.75 .72	.51 .25	.22 .64
								.90 .86	.86 .78	.79 .87	.81 .73	.73 .73	. 56 . 28	.20* .73
									.88 .85	.67 .75	.78 .88	.63 .82	.35 .32	.17 * .68
									-	.67 .65	.80 .80	.69 .79	.47 .37	.34 .63
										-	.79 .56	.78 .73	.60 .36	.17 * .82
												.83 .74	.57 .23	.33 .52
													.83 .69	.46 .72
														.43 .43

of freedom: 19. $5\,\%$ and $1\,\%$ levels of significance respectively.

	Plant height	Ear height	Leaves per plant	Leaves above ear	Ear leaf area	Tillers
02	33.04***	35.37 ***	1.34	9.09 ***	28.67***	42.73
	57.49***	66.29 ***	1.01	3.51	47.81***	1359.09
o_2 +	42.62***	35.66***	1.97 *	4.59*	40. 37***	248.51
	60.18***	56.32***	0.98	7.20***	49.74 ***	472.97
$\overset{o_2}{+}$	40.22***	34.55 ***	0.27	9.43 ***	41.37 ***	283.74
	28.63***	47.58 ***	4.86 ***	8.62***	40.1 3***	215.79
02	36.80***	29.64***	1.51	9. 28***	39.40 ***	18.18
	49.69***	58.17***	5.82 ** *	7.27 **	58.19 ***	17.86
02	58.78 ***	66.54 ***	-0.50	12.24***	48.09 ***	101.91
	57.77 ***	78.64 ***	4.69***	6.67**	54.41 ***	236.84
$\stackrel{o_{2}}{+}$	34.82*** 50.06***	31.99 *** 49.65 ***	0.76 - 0.49	6.90** 6.19**	38.83*** 43.02***	268.71 1679.75***
$\stackrel{o_2}{+}$	33.29 ***	41.80 ***	4.97 ***	7.96 ***	41.92***	147.79
	39.82 ***	47.81 ***	3.76 ***	9.62 ***	51.42***	3860.00 **
O_2 $+$	37.91***	40.33 ***	5.43 ***	9.62***	36.84 ***	-73.51
	59.19***	63.21 ***	4.74 ***	10.20***	56.9 2***	203.03
o_2 $+$	47.90 ***	66.32***	4.91 ***	12.38***	30.90 ***	182.64
	51.17 ***	59.26***	0.52	3.70	48.54 ***	4420.00**
o_2	35.82 ***	32.24***	1.77 *	4.06 *	44.68 ***	890.28
$+\cdot$	48.31 ***	57.68 ***	5.70 ***	11.30 **	43.01 ***	1903.70 **
o_2	37.99 ***	25.46 ***	2.86***	10.53 ***	43.25 ***	525.00
	53.43 ***	46.66 ***	4.06***	11.93 ***	52.08 ***	85.71
$\overset{o_2}{+}$	59.73 ***	58.40 ***	2.38**	14.78 ***	65.07 ***	1007.95 *
	52.74 ***	57.48 ***	1.00	9.24 ***	48.37 ***	603.70
02	34.53 ***	23.57***	4.39 ***	9.91***	35.00***	321.74
	44.31 ***	56.75***	10.67 ***	16.00***	40.72***	725.00
02	48.27 ***	55.81***	1.81*	8.93***	48.35***	1107.58 *
-+	45.96 ***	61.00***	4.97 ***	10.91***	57.22***	∞*
$\stackrel{o_2}{+}$	43. 2 9***	36.32***	0.97	14.56***	44.38 ***	-19.35
	50.89***	63.81***	5.95 ***	11.54***	64.29 ***	312.50
o_2	41.66	40.93	2.32	9.6 2	41.81	336.93
	49.98	58.02	3.88	8.93	50.39	1149.71
	$\begin{array}{c} -\cdot \\ o_{2} \\ + \\ o_{2} $	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	heightheight o_2 33.04^{***} 35.37^{***} -1 57.49^{***} 66.29^{***} o_2 42.62^{***} 35.66^{***} $+$ 60.18^{***} 56.32^{***} o_2 40.22^{***} 34.55^{***} $+$ 28.63^{***} 47.58^{***} o_2 36.80^{***} 29.64^{***} $+$ 28.63^{***} 66.54^{***} o_2 36.80^{***} 29.64^{***} -1^{-1} 57.77^{***} 78.64^{***} o_2 38.78^{***} 66.54^{***} o_2 33.29^{***} 41.80^{***} $+$ 59.06^{***} 49.65^{***} o_2 33.29^{***} 41.80^{***} $+$ 59.19^{***} 63.21^{***} o_2 37.91^{***} 59.26^{***} o_2 37.90^{***} 58.40^{***} o_2 37.99^{***} 58.40^{***} o_2 37.99^{***} 58.40^{***} o_2 37.99^{***} 58.40^{***} o_2 37.99^{***} 58.40^{***} a_2 45.3^{***} 23.57^{***} a_2 48.27^{***} 55.81^{***} o_2 43.29^{***} 56.32^{***} a_2 43.29^{***} 56.32^{***} a_2 43.29^{***} 56.32^{***} a_3 41.66 40.93	heightheightper plant o_2 33.04^{***} 35.37^{***} 1.34 $+$ 57.49^{***} 66.29^{***} 1.01 o_2 42.62^{***} 35.66^{***} 1.97^* $+$ 60.18^{***} 56.32^{***} 0.98 o_2 42.62^{***} 34.55^{***} 0.27 $+$ 28.63^{***} 47.58^{***} 4.86^{***} o_2 36.80^{***} 29.64^{***} 1.51 $+$ 49.69^{***} 58.17^{***} 5.82^{***} o_2 58.78^{***} 66.54^{***} -0.50 $+$ 57.77^{***} 78.64^{***} 4.69^{***} o_2 33.29^{***} 41.80^{***} 4.97^{***} a_2 37.91^{***} 36.32^{***} 0.76 $+$ 50.06^{***} 49.65^{***} -0.49 o_2 33.29^{***} 41.80^{***} 4.97^{***} a_2 37.91^{***} 40.33^{***} 5.43^{***} a_2 37.91^{***} 40.33^{***} 5.43^{***} o_2 37.90^{***} 66.32^{***} 0.52 o_2 37.99^{***} 52.46^{***} 2.86^{***} a_2 47.90^{***} 58.40^{***} 2.38^{***} $+$ 52.74^{***} 57.48^{***} 1.00 o_2 34.53^{***} 23.57^{***} 4.39^{***} a_2 59.73^{***} 58.40^{***} 2.38^{***} a_2 59.73^{***} 58.40^{***} 2.38^{***} a_2 43.29^{**	heightheightper plantabove ear o_2 33.04^{***}_{**} 35.37^{***}_{**} 1.34 9.09^{***}_{**} -1 57.49^{***}_{***} 66.29^{***}_{***} 1.01 3.51 o_3 42.62^{***}_{***} 35.66^{***}_{***} 1.97^*_{*} 4.59^*_{***} -1 60.18^{***}_{***} 56.32^{***}_{***} 0.98 7.20^{***}_{***} o_2 40.22^{***}_{***} 34.55^{***}_{***} 0.27_{*}_{*} 9.43^{***}_{***} -1 28.63^{***}_{***} 47.58^{***}_{***} 4.86^{***}_{***} 8.62^{***}_{***} o_2 36.80^{***}_{***} 29.64^{***}_{***} 1.51_{*} 9.28^{***}_{***} -1^{*}_{*} 57.77^{***}_{***} 72.64^{***}_{***} -0.50_{*}_{*} 12.24^{***}_{***} o_2 38.82^{***}_{***} 31.99^{***}_{***} -0.49_{*}_{*} 6.90^{***}_{**} o_2 33.29^{***}_{***} 41.80^{***}_{***} 4.97^{***}_{***} 9.62^{***}_{***} o_2 37.91^{***}_{***} 41.80^{***}_{***} 3.76^{***}_{***} 9.62^{***}_{***} o_2 37.91^{***}_{***} 49.33^{***}_{***} 4.91^{***}_{***} 10.20^{***}_{***} o_2 37.91^{***}_{***} 52.66^{***}_{**} $0.52_{*}^{***}_{*}$ 1.30^{***}_{*} o_2 47.90^{***}_{**} 52.24^{***}_{**} 1.77^{*}_{*} $4.06^{*}_{***}_{*}$ o_2 37.90^{***}_{**} 52.46^{***}_{**} 2.86^{***}_{**} $10.53^{***}_{***}_{*}_{*}_{*}$ o_2 $59.73^{***}_{$	heightheightper plantabove carleaf area o_2 33.04^{***} 55.37^{***} 1.34 9.09^{***} 28.67^{***} -1^{-1} 57.49^{***} 66.29^{***} 1.01 3.51 47.81^{***} o_2 42.62^{***} 35.66^{***} 1.97^* 4.59^* 40.37^{***} $+$ 60.18^{***} 56.32^{***} 0.98 7.20^{***} 49.74^{***} o_2 40.22^{***} 34.55^{***} 0.27 9.43^{***} 41.37^{***} $+28.63^{***}$ 47.58^{***} 4.86^{***} 8.62^{***} 40.13^{***} o_2 36.80^{***} 29.64^{***} 1.51 9.28^{***} 39.40^{***} $+$ 49.69^{***} 58.17^{***} 5.82^{***} 7.27^{**} 58.19^{***} o_2 36.80^{***} 29.64^{***} -0.50 12.24^{***} 48.09^{***} o_2 35.87^{***} 66.54^{***} -0.49 6.90^{***} 58.19^{***} o_2 34.82^{***} 31.99^{***} 7.96^{***} 41.92^{***} o_2 37.91^{***} 40.33^{***} 4.97^{***} 9.62^{***} 51.42^{***} o_2 37.91^{***} 40.33^{***} 5.43^{***} 9.62^{***} 51.42^{***} o_2 37.91^{***} 40.33^{***} 4.97^{***} 10.20^{***} 56.92^{***} o_2 47.90^{***} 66.32^{***} 4.91^{***} 10.20^{***} 56.92^{***} o_2 47.90^{***} 66.32^{***} <td< td=""></td<>

Table 3. Percent heterosis observed for various characters in the opaque-2

*, **, *** indicate significance at 5%, 1% and 0.1% levels of significance respectively.

been found to show significant differences due to opacity, it will be observed that in about two-thirds of the cases a poorer correlation occurs in the presence of the o_2 gene than in its absence. It will still, however, be found that the grain yield of opaque-2 types is more favourably correlated with the kernels per row than is grain yield of the normal types (Table 2). Similarly, kernels per row displays a stronger correlation with rachis weight, and so do kernels per ear with kernel rows, kernel rows with rachis diameter and total leaves with drying percentage of the ear, with the opaque-2 maize than with the normal maize.

Heterosis

Average heterosis observed for each of the opaque-2 single cross hybrids and their normal analogues is presented in Table 3. In most cases the extent of heterosis observed is greater for a cross made between normal inbred lines than for that between their opaque-2 analogues. This holds true in nearly 60 percent of the cases. There is also tremendous variation among hybrids and characters. Some of the characters show better heterosis in the presence of the o_2 gene than in its absence. The examples are earlier male and female flowering, a greater number of kernel rows, higher shelling percentage, larger kernels in length and width, heavier kernels and higher kernel density. Conversely, the overall grain yield shows a much poorer heterotic response when the endosperm is of the opaque-2 type than when normal. There are only two hybrids (N6 $o_2 \times$ W187 o_2) and (C103 $o_2 \times$ W187 o_2) which show more heterosis for grain yield in the presence of the o_2 gene than in their normal analogues. The characters, ear height, ear leaf area, raw ear yield, ear length, kernels per row, kernels per ear and rachis weight also show a similar trend.

31.96

37.15

Days to 50%	Days to 50%	Number	Raw	Drying	Shelling	Grain	Ear	Ear
pollen shed	silking	of ears	ear yield	‱-age of ear	^{0/} / ₀ -age	yield	length	diameter
— 5.63***	— 5.40***	10.45	79.53 ***	-3.04	4.9 2	72.98 **	23.02***	12.77**
—11.41***	— 9.63***	61.48	391.99 ***	-10.63	16.40**	384.34 ***	72.90***	41.76***
— 10.48***		62.44	276.81***	— 9.16	9.72*	251.67***	52.89***	32.47***
— 9.88***		95.78 *	668.48***	— 9.19	21.85**	759.85***	104.81***	47.10***
- 7.32***	— 7.51***	12.86	137.60***	0.99	6.13	136.97***	35.12***	24.09 ***
- 6.55***	— 7.29***	22.61	190.0 2** *	9.67	11.95 **	262.60***	46.76***	36. 22***
— 8.44 ***		79.73	361.70***	-10.26	39.73***	284.66***	44.56***	34.37 ***
— 7.66 ***		126.97 *	640.65***	- 5.52	20.08***	707.58***	71.14***	33.90 ***
		70.20 83.99	343.92 *** 483.39 ***	-13.85 - 16.88	22.19*** 12.68**	246.21*** 389.63***	44.76*** 75.05***	40.11*** 51.70***
- 6.76***	— 7.23***	32.86	125.54 ***	— 12.04	3.61	79.60	34.83 ***	19.82***
11.20***	— 7.86***	35.50	274.42 ***	— 9.96	20.25 ***	287.13***	57.84* * *	28.28***
1.31	— 1.88	12.52	89.54***	0.09	0.69	88.71***	34.97***	11.47 **
8.99***	— 7.72***	69.84	206.95***	14.16	9.99 *	284.82***	60.76***	31.09 ***
- 3.63 ***	-10.65***	43.57	175.10 ***	- 20.60	26.99***	83.09 ***	38.72***	26.40***
- 5.72 ***	- 8.22***	44.46	293.79 ***	- 6.68	11.01*	304.30 ***	60.66***	26.30***
7.01***	- 9.92***	40.89	149.71 ***	-3.93	10.83*	112.29 ***	28.00***	26.95***
10.41***	- 11.43***	29.52	310.27 ***	- 4.28	4.92	355.10 ***	59.86***	32.94***
7.43***	— 8.55 ***	32.83	166.51 ***	-4.27	8.69	150.50 ***	47.05 ***	13.60**
3.40***	— 4.69 ***	34.34	269.95***	1.67	17.30 ***	317.78 ***	56.75 ***	32.20***
		129.56 * 87.73	587.98*** 630.58***	-6.04 -12.38	34.39 *** 20.42 ***	595.61 *** 714.85 ***	76.30*** 64.29***	52.04*** 35.28***
- 8.95***		150.88 **	737.94 ***	— 14.96	21.74***	724.39***	90.09 ***	55.14 ***
- 8.20***		70.96	464.83 ***	— 16.67	11.07*	424.40***	76.24 ***	41.49 ***
8.56 *** 1.10		$54.26 \\ 32.62$	261.05*** 238.13***	1.94 11.34	37.70 *** 11.29 *	222.80*** 328.05***	57.89*** 52.70***	26.27 *** 29.86 ***
— 5.11***	— 9.57 ***	89.66 **	318.11 ***	— 0.99	16.31 ***	303.70 ***	64.05***	38.41 ***
4.93***	— 6.19 ***	41.71	286.41 ***	7.08	4.09	384.46 ***	77.07***	46.52 ***
		156.38 * 82.48	854.55*** 488.52***	3.27 - 3.15	56.80*** 8.95	908.72*** 517.24***	87.32*** 66.81***	65.46*** 42.64***

- 6.19

- 3.43

20.02

13.48

and the analogous normal single cross hybrids over their mid-parent values

Table 3 also demonstrates that many of the hybrids show statistically significant heterosis in the normal cross for a given character, whereas the heterosis observed in its opaque-2 counterpart is not significant, or vice versa, or one is significant at a higher level of significance than the other. Examining those showing differences between the o_2 and the normal types, it will be noted that some of the o_2 hybrids are definitely capable of giving greater heterosis than their normal analogues, for a number of characters, including several of the yield components. Thus, the o, hybrids showing increased heterosis over their normal counterparts, for a large number of characters at a time, are (N6 $o_2 \times$ W187 o_2), (HMv850-2 $o_2 \times$ W187 o_2) and (R61 $o_2 \times W187 o_2$). Similarly kernel rows and, to a lesser extent, shelling percentage are the characters favoured in a greater number of hybrids by the incorporation of the o_2 gene. The water imbibing capacity

65.27

61.33

7.82

7.37

-11.23- 8.68

311.04

389.22

of the kernels showing negative heterosis on an average is reduced to a larger extent and more frequently in the crosses of the normal type than in the o_2 type.

50,64

66.91

284.13

428.14

Discussion

A comparison of the crosses of the type made in the present investigations, that is, by studying the differences in the crosses made between the o_2 converted and the normal analogous inbred lines, makes possible a precise understanding of o_2 gene effects in the recessive homozygous condition. The elaborated studies of earlier workers have lacked this aspect (Sreeramulu and Bauman, 1970; Salamini et al., 1970).

The results presented above clearly show that improvement in the recessive homozygotes is possible for all the characters, including grain yield. Although a large number of correlation coefficients are of poorer

70

Table 3 (continued)

Hybrid	Kernel rows		Kernels per row	Kernels per ear	Rachis weight	Rachis diameter	Kernel length
1. WF9 × R61	02 +	5.60 18.81***	23.74*** 84.10***	30.91*** 116.09***	56.11*** 207.81***	11.37 39.95	14.28 * 41.46 ***
2. WF9 × N6	O_2	13.93** 19.21***	51.56*** 89.66***	72.56*** 123.30***	174. 27*** 349.96 ***	22.49 53.18	40.19 *** 37.19 ***
3. WF9 \times HMv850-2	$\overset{o_2}{+}$	18.70*** 13.19**	35.83 *** 56.37 ***	61.10*** 75.07***	87.59*** 164.87***	16.37 41.24	38.46*** 29.13***
4. WF9 \times C103	02 ⊣-	20.73*** 19.55***	54.24 *** 72.89 ***	83.41 *** 107.73 ***	180.04*** 328.36***	23.38 39.73	55.56 *** 24.56 **
5. WF9 × W187	o_2 +-	15.42 ** 8.24 *	51.21*** 84.91***	70.58*** 101.43***	107.26*** 211.19***	34.70 73.85	48.57 *** 40.00 ***
6. R61 × N6	02 ↓-	11.40** 11.34*	34.63*** 61.8 2***	49.36*** 79.07 ***	116.67 *** 154.79 ***	24.45 23.08	13.43* 33.93***
7. R61 × HMv850-2	0 2 ∔-	1.73 10.22*	34.42*** 67.83***	36.50*** 85.17***	86.53*** 176.27***	12.74 20.26	8.33 49.15 ***
8. R61 × C103	$\overset{o_2}{+}$	15.81** 10.12*	35.49 *** 67.82***	53.13 *** 84.61 ***	121.99*** 219.14***	26.88 19.20	23.08** 39.05***
9. R61 × W187	$\overset{o_2}{+}$	14.21** 8.40*	40.43 *** 47.58 ***	55.50*** 111.32***	121.81*** 192.27***	33.33 45.77	19.70 ** 53.15 ***
10. N6 × HMv850-2	o_2 +	14.07 ** 8.04	58.63 *** 43.88 ***	80.15*** 92.09***	140. 22*** 182.85 ***	5.99 28.54	27.12*** 36.21***
11. N6 \times C103	o_2 +	2 8.06 *** 10.50 *	73.43 *** 84.23 ***	120.91*** 104.64***	446.39 *** 381.74 ***	50.00 30.41	53.85*** 43.69***
12. N6 × W187	$\overset{o_2}{+}$	27.16*** 3.10	96.89 *** 89.29 ***	145.59 *** 99.32 ***	378.87*** 301.44***	63.97 54.90	43.40*** 21.10*
13. HMv850-2 × C103	$\stackrel{o_{2}}{+}$	22. 01 *** 8.93	71.58*** 76.05***	105. 16*** 94.09 ***	182.24*** 247.31***	18.43 25.69	40.59 *** 35.78 ***
14. HMv850-2 \times W187	o_2 +	17.23*** 4.50	82.60*** 116.31***	109.48*** 129.73 ***	218.44*** 295.42***	33.87 50.45	46.55 *** 40.87 ***
15. C103 \times W187	02 -+-	17.98** 2.64	102.38*** 95.83***	141.32*** 100.50***	425.78*** 381.90***	57.76 48.92	77.53 *** 33.33***
Average	$\overset{o_2}{+}$	16.27 10.10	56.47 75.90	81.04 100.28	189.61 253.02	29.05 39.68	36.71 37.23

value in the opaque-2 genotypes than in the normal, the present analysis shows that an advance in selection can be predicted using the opaque-2 maize because it demonstrates a better correlation than does normal maize between such characters as grain yield and kernels per row, kernels per row and rachis weight, kernels per ear and kernel rows, kernel rows and rachis diameter, and total leaves and drying percentage of the ear.

The data presented on heterosis in the o_2 and the analogous normal hybrids seem to be as promising as the data on correlation coefficients. Thus, the characters kernel rows and shelling percentage are more favoured by the o_2 gene in a number of hybrids.

Kernel	1000 grain	Kernel	$\frac{0}{20}$ water imbibed
width	weight	density	
4.29	23.12**	6.67	- 9.46
19.38***	34.69***	1.82	- 19.53*
18.40***	69.88***	2.56	- 7.99
13.60***	56.22***	6.33	- 19.24 *
9.77 **	19.17*	-3.38	-13.03
12.31 **	20.31*	-0.58	- 5.97
10.93 **	29.72**	7.50	25.71*
16.42 ***	47.82***	12.42*	- 6.56
25.62***	55.88***	11.39	-16.62*
16.13***	38.52**	4.35	- 5.06
6.77	28.05**	7.79	1.38 - 11.55
15.62 ***	32.95**	11.24*	
6.38	11.56	2.27	— 5.18
17.29 ***	43.24***	4.35	— 21 .97 *
11.76**	4.44	7.59	25.42*
18.25***	25.48 **	7.32	
17.83***	16.90	8.97	-23.15**
14.96***	20.64*	2.32	-31.73***
19.05***	52.44 ***	18.42 **	- 9.09
11.63**	34.75 ***	3.95	- 17.05*
23.97***	65.85***	$\begin{array}{r}13.43\\4.46\end{array}$	— 8.64
21.80***	55.96***		— 19.38**
28.07 ***	115.86***	27.27 ***	— 1.94
12.20 **	39.20***	4.24	— 17.48 *
28.68*** 15.94***	29.31** 18.66*	7.69 - 5.81	$-\frac{14.14}{0.70}$
24.59***	47.66***	14.28*	-4.13
15.62***	24.14**	— 1.11	-20.60*
36.79 ***	74.32***	10.29	-10.67
21.21 ***	40.40***	12.50*	-13.61
18.19	42.94	9.52	-2.88
16.16	35.53	3.95	-15.40

Received December 22, 1973 Communicated by L. Alföldi In addition, each of the characters, and particularly the maturity characters and the yield components, is favoured by the o_2 gene in one or other of the hybrids. Similarly, each of the o_2 hybrids shows a better heterotic response than its normal analogue for one or other of the characters.

Literature

- Alexander, D. E., Lambert, R. J., Dudley, J. W.: Breeding problems and potentials of modified protein maize. In: New approaches to breeding for improved plant protein, 55-65. Vienna: International Atomic Energy Agency 1969.
- Emerson, R. A., Beadle, C. W., Fraser, A. C.: A summary of linkage studies in maize. Cornell Univ. Agr. Expt. Sta. Mem. 480 (1935).
- Feist, W. A., Lambert, R. J.: Changes in six different opaque-2 genotypes of Zea mays L. during successive generations of backcrossing. Crop Sci. 10, 663-665 (1970).
- Fisher, R. A.: Applications of Student's distributions. Metron 5, 90-104 (1926).
- Gupta, D., Kovács, I.: A physiological study of opaque-2 maize and its normal analogue. Proceedings of the VII meeting of the maize and sorghum section of Eucarpia joint physiology section, Stubičke Toplice, Yugoslavia, September 3-6, 1973, in press (1974a).
- Gupta, D., Kovács, I.: Kernel characteristics of opaque-2 maize and its normal analogue. *ibid.* (1974b).
- Lambert, R. J., Alexander, D. E., Dudley, J. W.: Relative performance of normal and modified protein (opaque-2) maize hybrids. Crop Sci. 9, 242-243 (1969).
- Salamini, F., Borghi, B., Lorenzoni, C.: The effect of the opaque-2 gene on yield in maize. Euphytica 19, 531-538 (1970).
- Snedecor, G. W.: Statistical methods. Ames, Iowa: Iowa State College Press 1956.
- Sreeramulu, C., Bauman, L. F.: Yield components and protein quality of opaque-2 and normal diallels of maize. Crop Sci. 10, 262-265 (1970).

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