

RELATIVE GENETIC POTENTIAL OF BRACHYTIC MAIZE (*Zea mays* L.) VARIETIES AS BREEDING POPULATIONS

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ABSTRACT

Six brachytic maize (*Zea mays* L.) varieties were evaluated in diallel cross. The six varieties, the fifteen intervarietal hybrids and two checks were evaluated in a randomized block design with six replications at one location. The statistical-genetical analyses were performed according to the model proposed by Gardner and Eberhart (1966). Relative to the mid-parent, average heterosis was 0.8596 t/ha (17.09%), ranging from 0.150 t/ha (2.46%) to 2.221 t/ha (49.25%). The results showed that the varieties are genetically different both in terms of performance and heterotic potential. Significant specific heterosis was observed for plant height and ear height, which can be explained by the genetic diversity of the varieties with respect to the modifier genes containing some degree of dominance. The *Piranão VD-1* and *Piranão VF-1* varieties showed outstanding yielding ability both *per se* and in crossing. The hybrid between these two varieties showed the highest yielding ability of all diallel crosses. The heterosis level of this particular cross (13.79%) provided evidence of the presence of genetic diversity between the parental varieties, and these varieties are recommended for use in medium-term programs involving inbred line hybrids as well as in long-term programs of reciprocal recurrent selection.

INTRODUCTION

Most maize (*Zea mays* L.) germplasm in tropical regions involve tall plants, which cause serious lodging problems with consequent harvest losses. Because of this fact, breeders have been selecting for shorter plant germplasms using the polygenic

genetic variability of populations and on the basis of the major genes. Among the major genes the most appropriate is the recessive brachytic gene (br_2) which causes shortening of stalk internodes, thus reducing plant height (Bandel, 1978).

The choice of populations to be used in inter or intrapopulational breeding programs should be based on their relative performance both *per se* and in crosses, which can best be determined by methods involving diallel crosses. Lonnquist and Gardner (1961), Hallauer and Eberhart (1966), Hallauer and Sears (1968), Hallauer (1972) and Napolini Filho *et al.* (1981) have used diallel crosses for evaluating the relative genetic potential of open-pollinated varieties of maize as breeding populations.

At the Department of Genetics of ESALQ, Piracicaba, SP, Brazil, six brachytic maize varieties have been obtained by introducing the br_2 gene into tall plant varieties. These brachytic varieties have shown promise because of their high yielding ability and great lodging reduction (Paterniani *et al.*, 1977; Miranda Filho, 1979; Rissi and Paterniani, 1981; Castro, 1983). However, even though they have been used in several breeding programs, their relative genetic potential *per se* and in crosses is not known. Thus, the present study was undertaken to evaluate the six brachytic maize varieties in diallel crosses to obtain data which may be of help in the choice of populations to be used in breeding programs.

MATERIALS AND METHODS

Six open-pollinated brachytic maize populations that included the recessive br_2br_2 were used. They are referred to as varieties and designated as V_1 through V_6 . A brief description of the varieties follows:

V_1 - *Piranão VD-1* is a yellow dent variety obtained from a cross between *Piramex* and brachytic (br_2br_2) *Tuxpeño* obtained at CIMMYT, and by subsequent selection after the F_2 generation for brachytic types.

V_2 - *Cimmyt-br₂* is an orange flint variety obtained from a sample of maize homozygous for the br_2 gene received from CIMMYT.

V_3 - *Piranão VF-1* is an orange flint variety obtained from the cross between *ESALQ-VF-1* and *Cimmyt-br₂*, and subsequent backcross to *ESALQ-VF-1* followed by selection for brachytic types.

V_4 - *Piranão VD-2* is a yellow dent variety obtained from the cross between *ESALQ-VD-2* and *Piranão VD-1* and subsequent backcross to *ESALQ-VD-2* followed by selection for brachytic types.

V_5 - *Composto H.S. Dent br₂* is a yellow dent variety obtained from the intercross of single-cross hybrids. The br_2 gene was introduced through backcross by using *Piranão VD-1* as donor followed by selection for brachytic types.

V_6 - *Composto H.S. Flint br₂* is an orange flint variety obtained from the intercross

of single-cross hybrids. The br_2 gene was introduced through backcross by using *Cimmyt br_2* as donor followed by selection for brachytic types.

Checks - *AG-305-B* is a yellow semi-dent single-cross brachytic hybrid from Sementes Agroceres S/A and
AG-7811 - is a yellow semi-dent three-way-cross brachytic hybrid from Sementes Agroceres S/A

In March 1979, the six varieties were grown in all possible combinations in 30 m-long paired rows of 150 plants each. During inflorescence all possible crosses were made between varieties using a tassel not more than twice at pollen collection. Multiplication of the varieties was made through sib-crosses in a separate block. After harvesting, the same number of grains per ear was taken from each cross and each variety.

The six varieties, the 15 intervarietal hybrids, and both checks were evaluated in the agricultural year 1979/80 in a randomized complete block design with 6 replications in Piracicaba, State of São Paulo. Plots were 10 m long rows spaced 1.0 m, with hills spaced 0.20 m, with one plant per hill after thinning (50,000 plants per hectare). Data were obtained for plant height and ear height from a sample of 10 competitive plants within each plot approximately 20 days after flowering. Data for grain weight per plot were taken at harvest and adjusted to an ideal stand of 50 plants and 15.5% moisture.

Preliminary analyses of variance were performed according to the experimental design used for all three traits, with the entries being partitioned as varieties, intervarietal hybrids, checks, and among groups.

The genetic analyses were performed using the statistical genetical model proposed by Gardner and Eberhart (1966) which is appropriate for analyzing diallel crosses. The model is:

$$Y_{ij} = u + 1/2(V_i + V_j) + \theta(\bar{h} + h_i + h_j + s_{ij}), \text{ where}$$

u - is the mean of the varieties;

V_i or V_j - is the variety effect of variety i or j ;

\bar{h} - is average heterosis;

h_i or h_j - is variety heterosis, which is a contribution to the heterosis effect from variety i or j ;

s_{ij} - is specific heterosis or specific combining ability between varieties i and j ; and

$\theta = 0$ for $i = j$ and, $\theta = 1$ for $i \neq j$.

The sums of squares of the analyses of variance and the estimates of the genetic parameters of the means were calculated by the procedures described by Gardner (1967).

RESULTS AND DISCUSSION

The introduction of the br_2 gene in normal varieties considerably reduces plant and ear height by shortening stalk internodes (Castro, 1983). The varieties showed very reduced height ranging from 1.95 m (*Piranão VD₁*) to 1.57 m (*Composto H.S. Flint br₂*) for plant height, and from 1.22 m to 0.85 m for ear height. The intervarietal hybrids exhibited variation from 1.93 m ($V_1 \times V_4$) to 1.62 m ($V_2 \times V_4$) for plant height. According to Leng (1957), Anderson and Chow (1963), and Scott and Campbell (1969), apart from the major gene (br_2), there are polygenic inherited modifier genes affecting plant and ear height; the reduction in these traits can vary because of the different combinations of modifier genes of the genotypes where the br_2 gene is incorporated. This observation was confirmed in this research, because there were significant differences ($P < 0.01$) among varieties for these traits. For plant height we observed an average heterosis of 0.0371 m (2.24%), ranging from -0.105 m (\hat{h}_{24}) to 0.142 m (\hat{h}_{36}); for ear height, the average heterosis was 0.030 m (3.14%), ranging from -0.100 m (\hat{h}_{24}) to 0.088 m (\hat{h}_{56}).

Relative to the mid-parent, average heterosis for yield was 0.8596 t/ha (17.09%) ranging from $\hat{h}_{34} = 0.150$ t/ha (2.46%) to $\hat{h}_{26} = 2.221$ t/ha (49.25%) (Table I). These heterosis values are comparable to those obtained by Eberhart (1971), Hallauer (1972), and Hallauer and Malithano (1976). Relative to the high parent, average heterosis was 0.254 t/ha (4.88%), ranging from $\hat{h}_{45} = -0.535$ t/ha (-8.46%) to $\hat{h}_{26} = 1.441$ t/ha (27.25%). Moll *et al.* (1962, 1965) found that there is close relationship between the heterosis magnitude and the genetic diversity of the parental varieties. The magnitude of the heterosis relative to the midparent (h_{mp}) observed in crosses between populations is directly proportional to the differences of genic frequencies of the populations at loci which have some degree of dominance, i.e., $h_{mp} = \sum_i (p_i - r_i)^2 d_i$ (Falconer, 1960), where p_i and r_i are the frequencies of the favorable alleles in both populations, and d_i is the dominance effect. Cress (1966) concluded that the absence of heterosis does not necessarily mean lack of genetic diversity, because the dominance effects may be cancelled if they are not unidirectional, but the presence of heterosis means evidence of genetic diversity. The significance for heterosis ($P < 0.01$) in the analysis of variance (Table III) suggests the existence of high amplitude of heterosis variation for grain yield, indicating that there are variety pairs with different degrees of genetic diversity which can be used in synthesis of composites and, regarding the loci with some degree of dominance, may potentially increase the genetic variability for grain yield. No significance ($P < 0.05$ test F) was detected between checks for all traits evaluated; also, no significance was detected among intervarietal crosses for grain yield in the preliminary analysis of variance (Table II).

The performance of an intervarietal hybrid represents the average performance of all possible hybrids (single, double, or three-way) from crosses among inbred lines

Table I - Grain yield (t/ha) of the varieties (on the diagonal) and intervarietal hybrids (above the diagonal); values and significance^a of heterosis relative to the mid-parent (below the diagonal) and of heterosis relative to the high-parent (in parentheses-below the diagonal)

	Varieties ^b					
	V ₁	V ₂	V ₃	V ₄	V ₅	V ₆
V ₁	6.378	6.085	6.949	6.760	6.628	6.114
V ₂	(-0.293) 1.032**	3.729	6.330	5.842	5.898	6.729
V ₃	(0.571) 0.842*	(0.494) 1.548**	5.836	6.229	5.940	6.303
V ₄	(0.382) 0.410	(-0.481) 0.816*	(-0.094) 0.150	6.323	5.788	6.279
V ₅	(0.250) 1.007**	(1.033*) 1.601**	(0.104) 0.590	(-0.535) 0.194	4.865	6.035
V ₆	(-0.234) 0.311	(1.441**) 2.221**	(0.467) 0.741*	(-0.040) 0.474	(0.747) 0.959**	5.288

Checks: AG-305-B: 8.232 t/ha — AG-7811: 7.660 t/ha

^a Obtained by comparing heterosis values with zero by the t test.

^b V₁, V₂, V₃, V₄, V₅ and V₆ are Piranão VD-1, Cimmyt-br₂, Piranão VF-1, Piranão VD-2, Composto H.S. Dent-br₂ and Composto H.S. Flint-br₂, respectively.

*P < 0.05; **P < 0.01.

of the parental varieties. Thus, the presence of a high-yielding intervarietal hybrid shows that one can expect selected hybrids from crosses among inbred lines of each population to highly exceed the behavior of the intervarietal hybrid. Although the analysis of variance (Table II) showed no significance among the intervarietal hybrids, *Piranão VD-1* x *Piranão VF-1* (6.949 t/ha) was the highest yielding, and these varieties also exhibited high yielding ability *per se* (Table I). Thus, they are recommended to be used in medium-term programs for inbred line hybrids as well as in long-term programs for reciprocal recurrent selection, since the heterosis level in this particular cross ($\hat{h}_{13} = 0.842$ t/ha or 13.79%) indicates the existence of a high genetic diversity between parental varieties. Intervarietal hybrid breeding, after some cycles of selec-

tion, will improve the hybrids obtained from crosses between the inbred lines from the already improved varieties.

Table II - Values and significances of mean squares obtained in the analyses of variance for grain yield, plant height and ear height.

Sources of variation	d.f.	Mean squares		
		Grain yield (t/ha)	Plant height ($\times 10^{-2}$) (m)	Ear height ($\times 10^{-2}$) (m)
Blocks	5	1.245*	3.382**	1.782**
Entries	(22)	4.645**	5.856**	5.006**
Varieties	5	6.108**	12.438**	10.479**
Intervarietal crosses	14	0.777 ^{ns}	3.774**	3.335**
Checks	1	0.981 ^{ns}	0.152 ^{ns}	0.013 ^{ns}
Among groups	2	29.888**	6.827**	5.511**
Error	110	0.517	0.655	4.416
Coefficient of variation (C.V.%)		11.63	4.63	6.15

* $P < 0.05$; ** $P < 0.01$; ns, nonsignificant.

Heterosis can only be taken into account for commercial purposes if it is positive in relation to the high parental variety, i.e., when the hybrid surpasses the highest yielding parental population. Relative to the high-parent, heterosis is expressed as:

$$h_{ps} = \sum_i (r_i - p_i) \alpha_i,$$

where r_i and p_i are the frequencies of the favorable alleles in the low and high populations, respectively, and α_i is the average effect of a genic substitution in the high population (Souza Jr., 1983). Thus, for h_{ps} to be positive it is necessary that the favorable alleles whose frequencies are low in the high population have high frequencies in the low population. Hence, the low population complements the high population and the hybrid developed from their cross will have many more accumulated favorable genes than the high-parent. The highest yielding intervarietal hybrid *Piranão VD-1* x *Piranão VF-1* exhibited a heterosis of $h_{ps} = 0.571$ t/ha (8.95%) relatively to the high parental variety *Piranão VD-1*; thus, this intervarietal hybrid can be utilized for commercial purposes.

The values and significance of the mean squares obtained in the analyses of variance of the diallel tables, and the estimated means of the genetic parameters, according to the model proposed by Gardner and Eberhart (1966) are included in Tables III, IV and V, for the three traits.

Table III - Values and significances of mean squares obtained in the analyses of variance of diallel crosses for grain yield, plant height and ear height.

Sources of variation	d.f.	Mean squares		
		Grain yield (t/ha)	Plant height (m)	Ear height (m)
Populations	(20)	0.5034**	0.0099**	0.0085**
Varieties	5	0.8168**	0.0300**	0.0267**
Heterosis	(15)	0.3990**	0.0032**	0.0024**
Average heterosis	1	3.1655**	0.0059**	0.0039**
Variety heterosis	5	0.3612**	0.0028**	0.0010 ^{ns}
Specific heterosis	9	0.1127 ^{ns}	0.0031**	0.0030**
Error mean	110	0.0862	0.0011	0.0007

**P < 0.01; ns, nonsignificant.

The analyses of variance of the diallel tables for grain yield and plant and ear height indicated significances ($P < 0.01$) for variety effects. *Piranão VD-1* ($\hat{V}_1 = 0.974$ t/ha) was the highest yielding variety, whereas *Cimmyt br₂* ($\hat{V}_2 = -1.674$ t/ha) was the lowest; for plant and ear height *Piranão VD-1* and *Composto H.S. Flint br₂* were the tallest and the shortest, respectively.

For grain yield, the partition of heterosis effects in the analysis of variance (Table III) showed significance ($P < 0.01$) for average heterosis and variety heterosis, indicating that there are differences among observed values of heterosis. These differences are due to the fact that some varieties determine a particular heterotic effect, causing certain values of heterosis to be different from the others, and not due to specific combining ability. Similar results, showing that the varieties differ among themselves as well as to their heterotic potential in crosses due to the significance of variety effects, average heterosis and variety heterosis, have been reported by Hallauer and Eberhart (1966), Barriga and Vencovsky (1973) and Miranda Filho (1974).

For plant height, all heterosis components were significant and for ear height only the variety heterosis component was nonsignificant in the analyses of variance (Table III). These results differ from those reported by Barriga and Vencovsky (1973)

Table IV - Estimates of variety effect (\hat{v}_j), variety heterosis (\hat{h}_j), average of varieties (\hat{u}), and average heterosis (\hat{h}) for grain yield, plant height, and ear height.

$\hat{v}_{j,s}$	Grain yield (t/ha)	Plant height (m)	Ear height (m)	$\hat{h}_{j,s}$	Grain yield (t/ha)	Plant height (m)	Ear height (m)
\hat{v}_1	0.974	0.219	0.196	\hat{h}_1	-0.174	-0.018	-0.008
\hat{v}_2	-1.674	-0.108	-0.038	\hat{h}_2	0.730	0.000	-0.007
\hat{v}_3	0.433	0.024	-0.010	\hat{h}_3	-0.107	-0.007	0.001
\hat{v}_4	0.920	0.105	0.106	\hat{h}_4	-0.564	-0.054	-0.034
\hat{v}_5	-0.538	-0.162	-0.170	\hat{h}_5	0.013	0.022	0.031
\hat{v}_6	-0.115	-0.078	-0.084	\hat{h}_6	0.102	0.057	0.017
\hat{u}	5.403	1.729	1.020	\hat{h}	0.8596	0.0371	0.030

and by Miranda Filho (1974) who used normal varieties (taller and shorter polygenic varieties, respectively), and did not demonstrate statistical significance for specific heterosis for those traits. Even for grain yield, which is a more complex trait possessing a higher level of dominance, there are only a few reports showing significance for specific heterosis. Hallauer and Sears (1968), and Troyer and Hallauer (1968) detected specific heterosis significance for grain yield.

The presence of modifier genes with polygenic inheritance affecting the expression of the brachytic gene (br_2) can account for these results, because the modifier genes, being variables among the different varieties, cause a greater variation for plant and ear height among them. Hence, in crosses between too diverse varieties as to the modifier genes with some degree of dominance, differences among the degrees of complementation in the hybrid may occur. This would cause the appearance of the variation due to specific heterosis (specific combining ability).

Although specific heterosis effects were significant, the mean for plant and ear height in the intervarietal hybrids did not indicate discrepant values, since for the taller hybrid we observed 1.926 m and 1.208 m, and for the shorter one, 1.623 m and 0.954 m for plant and ear height, respectively. This occurred due the low plant and ear height heterosis values ($\hat{h} = 2.24\%$ and 3.14% , respectively), and since specific heterosis is a heterosis component, their contribution for determining the plant and ear height means of the hybrids is of low significance.

The sums of squares for grain yield were distributed in the following proportions: 40.6% for the variety effects and 59.4% for heterosis, with 31.4% for average heterosis, 17.9% for variety heterosis and 10.1% for specific heterosis. For plant height, we observed 76.0% for varieties and 24.0% for heterosis, with 3.0% for average hetero-

Table V - Estimates of specific heterosis (\hat{s}_{ij} 's) for grain yield, plant height, and ear height.

\hat{s}_{ij} 's	Grain yield (t/ha)	Plant height (m)	Ear height (m)	\hat{s}_{ij} 's	Grain yield (t/ha)	Plant height (m)	Ear height (m)
\hat{s}_{12}	-0.384	0.006	0.037	\hat{s}_{26}	0.529	-0.012	-0.016
\hat{s}_{13}	0.264	-0.062	-0.063	\hat{s}_{34}	-0.039	-0.002	0.003
\hat{s}_{14}	0.288	0.070	0.049	\hat{s}_{35}	-0.176	-0.040	-0.044
\hat{s}_{15}	0.308	0.016	0.020	\hat{s}_{36}	-0.114	0.054	0.031
\hat{s}_{16}	-0.476	-0.030	-0.043	\hat{s}_{45}	-0.115	0.007	0.018
\hat{s}_{23}	0.065	0.050	0.072	\hat{s}_{46}	0.076	0.014	0.019
\hat{s}_{24}	-0.209	-0.088	-0.089	\hat{s}_{56}	-0.016	-0.026	0.009
\hat{s}_{25}	-0.001	0.043	-0.003	-	-	-	-

sis, 7.0% for variety heterosis and 14.0% for specific heterosis. For ear height the sums of squares indicated a variation pattern similar to that for plant height: 78.8% for varieties and 21.2% for heterosis, with 2.3% for average heterosis, 2.9% for variety heterosis and 16.0% for specific heterosis. These results and the values observed for heterosis indicate the presence of considerable dominance effects in the control of grain yield, and for plant and ear height most of the loci controlling these traits must have additive genic effects. Hence, one can exploit heterosis for grain yield via intervarietal hybrids or via inbreeding hybridization as outlined by Shull (1909), without causing undesirable alterations in plant and ear height; the height of the hybrids will tend towards the average of the parental varieties due to the type of genic effects which controls these traits.

RESUMO

Foram avaliadas seis variedades de milho braquítico em cruzamentos dialélicos. As seis variedades, os quinze híbridos intervarietais e duas testemunhas foram avaliadas em blocos casualizados com seis repetições em um local. A análise estatístico-genética foi realizada segundo o modelo de Gardner e Eberhart (1966). A heterose média, em relação à média dos pais, foi de 0,8596 t/ha (17,09%), com amplitude de variação de 0,150 t/ha (2,46%) a 2,221 t/ha (49,25%). Os resultados indicam que as variedades diferem geneticamente entre si como tais e, também quanto ao seu potencial heterótico. Para os caracteres altura da planta e altura da espiga detectou-se significância para heterose específica, que pode ser explicado pela diversidade genética das variedades com relação aos genes modificadores com algum grau de dominância. As variedades *Piranão VD-1* e *Piranão VF-1* destacaram-se pelas elevadas produtividades *per se*, pelo híbrido intervarietal

com maior produtividade do conjunto e, a heterose neste cruzamento (13,79%) indica a existência de um bom nível de divergência genética. Em vista disso, recomendou-se o uso destas variedades em programas de híbridos de linhagens para médio prazo e, para serem utilizadas em programas de seleção recorrente recíproca a longo prazo.

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