

ESTIMATES OF COMBINING ABILITY FOR GRAIN YIELD IN MAIZE (*Zea mays* L.) POPULATIONS*

Delmar Brenner¹, Fernando I.F. de Carvalho² and Luis C. Federizzi²

ABSTRACT

Eight maize (*Zea mays* L.) populations and their 56 hybrids obtained by diallel crossing were tested for estimation of combining ability and other genetic parameters. The trial was grown in 1987 at the Experimental Station of the firm "Pioneer Agricultura Ltda." (Rio Pardo, State of Rio Grande do Sul, Brazil). The experimental design was an 8 x 8 duplicated simple lattice with 4 replications. Combining ability was estimated by Method 1, Model I of Griffing (*Aust. J. Biol. Sci.* 9: 463-493, 1956) which was used to partition the lattice-adjusted treatment mean squares into general combining ability (GCA), specific combining ability (SCA) and reciprocal effects (RE).

The results indicated that the populations are potential resources for breeding programs. Additive effects (GCA) were the most important. However, reciprocal and specific effects proved to be important in specific combinations.

INTRODUCTION

Maize selection programs have been effective in producing genotypes with greater grain yield potential and with agronomical traits more adapted to the technological changes constantly introduced in crop growing (Russel, 1974; Cardwell, 1982;

* Part of a thesis presented by D.B. to Universidade Federal do Rio Grande do Sul in partial fulfillment of the requirements for the Masters degree in Agronomy.

¹ Pioneer Agricultura Ltda., Caixa Postal 89, 96800 Santa Cruz do Sul, RS, Brasil.

² Universidade Federal do Rio Grande do Sul, Avenida Bento Gonçalves, 7712, Caixa Postal 776, 90001 Porto Alegre, RS, Brasil. Send correspondence to F.I.F.C.

Duvick, 1984a,b). However, progress has not been continuous, since periods of rapid gain have alternated with periods of stagnation. Advances in potential maize productivity have almost always been based on better knowledge of the genetical and biological principles involved, as well as on new methods and experimental and statistical techniques.

The development of lines for hybrid production and population breeding represents the basic strategies used in maize breeding. The two processes, which in the past were considered to be antagonistic, are currently being used in a complementary manner. There is no doubt that in the evolution of the various processes the greatest gain has been obtained by creating hybrid maize. The production of inbred lines and of hybrids is the major objective of current breeding programs in the more developed countries, and is acquiring increasing importance in the remaining parts of the world as more advanced technologies are adopted. Considering that the continuity of genetic gain is closely associated with the existence of genetic variability, it is necessary to introduce mechanisms for the creation and maintenance of an appropriate genetic base, in addition to preserving genes or traits that may be essential for agriculture in the near future. Among these mechanisms, population breeding may simultaneously provide the formation of new free-pollinating varieties and conditions of progress for the production of inbred lines for future hybrid formation. Eberhart (1971) emphasized that hybrid gain is proportional to the improvement of the populations utilized as a source of parental lines. The hybrid represents a genotype that can occur in a population whose lines have been identified and which therefore can be maintained and reproduced. Once the superior hybrids have been extracted from a population, the identification of crosses with a greater potential will only be possible by improving the source population. Lonquist (1963) and Jugenheimer (1976) pointed out that the main objective is the effective utilization of additive population variance before capitalizing on dominance and epistatic effects in specific combinations.

In view of these considerations, information about the genetic parameters of the populations involved is essential for the development of breeding programs. Knowledge about the mechanisms of trait or gene transfer, combining ability and maternal effects may directly help breeders to identify and produce superior lines, crosses or populations. The identification of open-pollinating maize (*Zea mays* L.) populations with genetic potential and the estimate of existing genetic parameters were the main objectives of the present study.

MATERIAL AND METHODS

Eight open-pollinating populations of distinct origins and their 56 hybrids obtained by diallel crossing were tested in 1987 in a trial at the Experimental Station of

Pioneer Agricultura Ltda. (Rio Pardo, State of Rio Grande do Sul, Brazil). The maize populations studied were:

1. Lorenzen - dent corn from Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA, Pelotas) which had not been submitted to strong selection pressure for the various agronomic traits.

2. Amarillo Del Bajío x Templados (P2) - semi-flint corn introduced from the International Center of Maize and Wheat Improvement (CYMMIT, Mexico) and submitted to several recurrent selection cycles by EMBRAPA (Pelotas).

3. Pool 33 (P3) - early semi-dent population originally introduced from CIMMYT (Mexico) and obtained from the Experimental Station of the Agricultural Department of Veranópolis.

4. Suwan-DMR (P4) - semi-flint corn introduced from CIMMYT (Mexico) through EMBRAPA where it is being submitted to recurrent selection.

5. Composto Amarelo Duro-RS/SC (P5) - a flint composite corn formed by the recombination of five regional maize varieties collected in the States of Rio Grande do Sul and Santa Catarina, obtained from EMBRAPA (Pelotas).

6. Composto Amarelo Dentado-RS/SC (P6) - a dent corn resulting from the recombination of 21 varieties collected by EMBRAPA in Rio Grande do Sul and Santa Catarina.

7. Asteca (P7) - a semi-dent population collected in the township of Estrela (Rio Grande do Sul) where it has been grown for many years.

8. Brasil (PB) - a dent population originating from the township of Taquari (Rio Grande do Sul).

The experimental design was an 8 x 8 duplicated simple lattice with four replications. Each plot consisted of two 5-meter rows spaced 0.80-meter apart. Plants were thinned to 18 per row, corresponding to 45,000 plants per hectare. Fertilizer was applied uniformly at sowing time (16 kg/ha N, 54 kg/ha P₂O₅ and 64 kg/ha K₂O) and again 35 to 40 days after seedling emergence (135 kg/ha N). Standard growing conditions were used throughout.

For the evaluation of population yield, grain moisture was corrected to 15.5%. For statistical analysis, treatment mean squares were determined using lattice-adjusted means and the residue was considered to be the effective lattice error calculated by the formula of Cochran and Cox (1965). In the analysis of population combining ability, lattice-adjusted treatment mean squares were partitioned into general combining ability (GCA), specific combining ability (SCA), and reciprocal effects (RE) by Method I, Model I of Griffing (1956). The same model was also used to estimate GCA effects associated with each parent (g_i), SCA effects (s_{ij}) and reciprocal effects (r_{ij}) associated with each cross. Heterosis estimates were obtained considering the following expression

$h_{ij} = 1/2 (y_{ij} + y_{ji} - y_{ii} - y_{jj})$. Statistical analysis and combining ability analysis were performed using the SAEG (U.F.V.) statistical program.

RESULTS AND DISCUSSION

The overall mean yield for the eight populations and the 56 crosses was 5797 kg/ha. Mean grain yield was 4984 kg/ha for the parental populations and 5913 kg/ha for the hybrids. This resulted in a mean heterosis of 927 kg/ha corresponding to an 18.6% gain.

Analysis of *per se* performance showed that populations P2, P4, P6 and P3 had the highest grain yields. However, all populations showed lower grain yields than the overall diallel mean. Population analysis for mean grain yield on the basis of the combinations of each population in the diallel cross as maternal and paternal lines showed that the populations of Mexican origin (P2, P3 and P4) were the most promising (Table I). All combinations within the Mexican group, except P2 x P4, produced higher yields than the diallel mean. It should also be pointed out that all crosses within the population group originating from Southern Brazil (P1, P5, P6, P7 and P8) showed lower grain yields than the overall mean, except for the combinations of population P7 with P5 and P6 and the P6 x P8 hybrid. However, the hybrids with the highest grain yields resulted from the combinations of the population groups (P7 x P3, P5 x P4, P2 x P1, P1 x P2, P1 x P3, and P4 x P6), a factor indicating that these population groups have potential for use in breeding programs.

Table I - Mean grain yield (kg/ha) of parental populations (diagonal), F1's (above the diagonal), and reciprocals (below the diagonal) in the four replications of an 8 x 8 duplicated simple lattice.

	P1	P2	P3	P4	P5	P6	P7	P8	FM
P1	5033	6620	6181	5845	5676	4931	5414	5685	5673.1
P2	6884	5737	5876	6385	6018	6038	6076	5985	6124.9
P3	6571	5851	5334	6311	6250	5985	7211	5442	6119.4
P4	6271	5635	6289	5553	7020	6227	6196	5721	6114.0
P5	4873	6085	5978	6198	4338	5626	6371	4568	5504.6
P6	5285	5835	5200	6890	5369	5425	6155	4910	5633.6
P7	5110	6187	6363	6213	6246	5983	4713	4724	5692.4
P8	5478	5841	5678	6479	5264	6114	5491	3752	5512.1
MM	5688.1	5973.9	5862.4	6234.3	5772.6	5791.1	5953.4	5098.4	5797.0

MM - Mother means; FM - Father means.

The analysis of the differences between treatments (at the 1% level of probability) showed that the existing variability mainly originated from the genetic differences between the populations *per se*, the crosses, and their interactions (Table II). In addition to detecting the availability of genetic variability, breeders should know the nature of the gene action and the mechanisms of transfer of these genes. This objective was fulfilled in the present study by analysis of combining ability, Table III which was done by determining the magnitude of mean squares (MS) for general combining ability (GCA) and specific combining ability (SCA). The mean square for GCA was 2.3 times the mean square for SCA. No significant differences at the 1% level of probability were detected for the reciprocal effects. The significant mean squares for GCA demonstrated the existence of populations which presented higher means in their crosses than other populations included in the diallel program. Furthermore, the significant mean squares for SCA showed that certain combinations were significantly superior or inferior than expected in terms of general combining ability. According to Sprague and Tatum (1942), genetic variability due to GCA originates from additive gene effects, while SCA originates from non-additive gene action, and more specifically from dominance and epistatic effects. Lonquist (1963, 1965) emphasized that population improvement by selection is directly related to additive gene action, while heterosis manifested in the combination of two varieties also depends on non-additive effects. Thus, the estimates obtained in the present study indicate that in a breeding program involving the populations evaluated, both additive and non-additive effects should be considered for maximum expression of heterosis.

Table II - Mean squares (M.S.) of the *populations* and its crosses.

Sources of variation	d.f.	M.A.
Adjusted treatments	63	1.716*
Parents	7	1.840*
Crosses	55	1.296*
Parents x Crosses	1	24.030*
Effective lattice error	161	0.525

* Significant at the 1% level of probability by the F test.

In addition to the analysis of the magnitude of the MS for the components of combining ability, the estimates of GCA effects associated with each parent (g_i) and of

SCA and RE effects associated with each cross (s_{ij} and r_{ij} , respectively) based on the model of Griffing (1956) permitted us to better identify the magnitudes of the various types of gene action involved. Analysis of Table IV shows that the populations of Mexican origin (P2, P3 and P4) revealed the greatest additive effects. Considering that these populations were the most promising ones and that they participated in all hybrids with the highest grain yields (P7 x P3, P5 x P4, P4 x P6, P1 x P2, P2 x P1, and P1 x P3), they generally confirmed the greater importance of genes with additive action. As a consequence of the high additive effects, populations P2, P3 and P4 seem to be the most indicated both for the extraction of inbred lines and for the inclusion in programs for the formation of synthetics or for the derivation of improved populations.

Table III - Mean squares (MS) of the combining ability components, of the effective lattice error, general mean and coefficient of variation for grain yield in eight parental populations and their 56 hybrids (Rio Pardo, 1987).

Sources of variation	d.f.	MS
Adjusted Treatments	63	1.716*
General Combining Ability (G.C.A.)	7	4.861*
Specific Combining Ability (S.C.A.)	28	2.094*
Reciprocal Effects (R.E.)	28	0.553*
Effective Lattice Error (E.L.E.)	161	0.525
General Mean [M (t/ha)]	5.797	
Coefficient of Variation [C.V. (%)]	12.5	

* Significant at the 1% level of probability by the F test.

With respect to specific effects (s_{ij}), it can be seen that all populations revealed negative values in terms of *per se* performance, indicating the superiority of the hybrids for grain yield (Table IV). Among the crosses, the low s_{ij} effects in the combinations within the parental group originating from Southern Brazil, taken together with the low general combining ability, led to grain yields lower than the overall diallel mean, except for the combinations of population P7 with P5 and P6 and the P6 x P8 hybrid. Similarly,

all combinations within the population group of Mexican origin (high general combining ability) revealed negative s_{ij} effects. This fact prevented the occurrence of the best alternative for a breeding program, i.e., the association of high g_i and s_{ij} effects in the same populations (Barrales *et al.*, 1973). However, considerable contributions to specific effects were detected in all the promising hybrids formed by combining the two population groups. The low specific combining ability within each group may indicate similar gene frequencies in the populations involved, while the relevance of specific effects in the combinations between the two groups may result from genetic divergence. This genetic divergence is confirmed by the heterosis estimates in Table V, showing high percentages for the best crosses. In addition, even though the MS of reciprocal effects were not significant, they should be considered in certain combinations such as P7 x P3 and P5 x P4, which revealed high r_{ij} values (Table IV).

Table IV - Estimates of specific combining ability (s_{ij}) of the populations (diagonal) and the crosses (above the diagonal) and estimates of reciprocal effects (below the diagonal) and the general combining ability (bottom of the table) for grain yield.

	P1	P2	P3	P4	P5	P6	P7	P8
P1	-0.531	0.819	0.501	0.000	-0.248	-0.488	-0.445	0.392
P2	-0.132	-0.565	-0.380	-0.417	0.160	-0.028	0.056	0.355
P3	-0.195	0.013	-0.851	-0.068	0.281	-0.314	0.770	0.061
P4	-0.213	0.375	0.011	-0.998	0.593	0.469	0.004	0.417
P5	0.401	-0.033	0.136	0.411	-1.142	-0.057	0.644	-0.231
P6	-0.177	0.101	0.392	-0.332	0.128	-0.203	0.331	0.291
P7	0.152	-0.056	0.424	-0.008	0.063	0.086	-1.136	-0.224
P8	0.104	0.072	-0.118	-0.379	-0.348	-0.602	-0.383	-1.062
g_i	-0.116	0.253	0.194	0.377	-0.158	-0.084	0.026	-0.492

Thus, the search for the best combinations in a breeding program should involve populations from the two groups. This procedure may lead to the association of the high additive effects (g_i) of the populations originating from Mexico with the high specific (s_{ij}) and reciprocal (r_{ij}) effects of the populations originating from Southern Brazil.

Table V - Heterosis estimates of the populations in t/ha (above the diagonal) and as a percentage of the mid parents (below the diagonal) for grain yield.

	1	2	3	4	5	6	7	8
1		1.367	1.193	0.765	0.589	-0.121	0.389	1.189
2	25.4		0.328	0.355	1.014	0.356	0.907	1.169
3	23.0	5.9		0.857	1.278	0.213	1.764	1.017
4	14.5	6.3	15.7		1.664	1.070	1.072	1.448
5	12.6	20.1	26.4	33.6		0.616	1.783	0.871
6	-2.3	6.4	4.0	19.5	12.6		1.000	0.924
7	8.0	17.4	35.1	20.9	39.4	19.7		0.875
8	27.1	24.6	22.4	31.1	21.5	20.1	20.7	

Average heterosis - 18.6%.

CONCLUSIONS

The potential productivity and genetic variability of the different maize populations tested recommend their use in improvement of the species. Furthermore, the superior development of the hybrids obtained and the heritability mechanism based on general combining ability indicate the possibility of genetic gain in many of the populations tested through any type of selection system, whether mass or recurrent.

The favorable additive action, more intensely expressed in the populations of Mexican origin, permits the inclusion of these populations in programs for the formation of inbred lines, open-pollinating varieties and synthetics. The fact that greater vigor was detected in hybrids from the crosses of the populations of Mexican origin with material from the South of Brazil indicates the need to include both additive and non-additive effects in genetic combinations in order to favor the interaction of different gene actions in the expression of heterosis. The identification of maternal effects in some populations by combination of their progenies also permits the breeder to select the best mechanism for hybrid formation.

RESUMO

Oito populações e seus 56 híbridos, formados através de um cruzamento dialélico, foram avaliados com relação a capacidade combinatória e outros parâmetros genéticos. O experimento foi instalado na Estação Experimental da Empresa Pionner Agricultura Ltda (Rio Pardo, RS) no ano agrícola de 1987. O delineamento

experimental utilizado foi o Lattice simples duplicado 8x8 com 04 repetições. A capacidade combinatória foi estimada pelo Método 1, Modelo 1 de Griffing (Aust. J. Biol. Sci. 9: 463-493, 1956). Por este método a soma de quadrados dos tratamentos foi decomposta em capacidade geral (C.G.C.), específica de combinação (C.E.C.) e efeitos recíprocos (E.R.).

Os resultados evidenciaram que as populações possuíam potencial para serem utilizados programas de melhoramento. Os efeitos gênicos aditivos (C.G.C.) foram os mais importantes; contudo, foram detectados efeitos específicos (C.E.C.) e recíprocos (E.R.O) em determinadas combinações.

REFERENCES

- Barrales, V.L., Barnier, B.R. and Violic, M.A. (1973). Análises de cruzamientos dialelos en maiz mediante el Método de Griffing. *Agricultura Técnica* 33: 36-43.
- Cardwell, V.B. (1982). Fifty years of Minnesota Corn yield increase. *Agronomy Journal* 74: 984-990.
- Cochran, W.G. and Cox, G.M. (1965). *Diseños Experimentales*. México, A.I.D. 661 p.
- Duvick, D.N. (1984a). Progress in conventional plant breeding. *Proceedings of Stadier Genetic Symposium*, 16. p. 17-31.
- Duvick, D.N. (1984b). Genetic contributions to yield gains of U.S. hybrid maize, 1930 to 1980. In: *Genetic Contributions to Yield Gains of Five Major Crop Plants* (Fehr, W.R., ed.). Madison, American Society of America. pp. 15-47.
- Eberhart, S.A. (1971). Techniques and methods for more efficient population improvement in Sorghum. In: *Sorghum in the Seventies* (House, L.R. and Rao, N.G.P., eds.). pp. 196-213.
- Griffing, B. (1956). Concept of general and specific combining ability in relation to crossing systems. *Austr. J. Biol. Scien.* 9: 463-493.
- Jugenheimer, R.B. (1976). *Corn Improvement. Seed Production and Uses*. New York, John Wiley & Sons. 670 p.
- Lonnquist, J.H. (1963). Gene action and corn yields. *Hybrid Corn Industry-Research Conference*. American Seed Trade Association. pp. 37-44.
- Lonnquist, J.H. (1965). Métodos de selección útiles para mejoramiento dentro de poblaciones. *Fitotecnia Latinoamericana* 2: 1-10.
- Patemiani, E. and Miranda Filho, J.B. (1987). Melhoramento de populações esesese In: *Melhoramento e Produção de Milho*. (Patemiani, E. and Viegas, G.P., eds.). Campinas, Fundação Cargill. v.1. pp. 217-274.
- Russel, W.A. (1974). Comparative performance for maize hybrids representing different eras of maize breeding. *Report of Annual Corn Sorghum Research Conference*. Chicago, American Seed Trade Association. pp. 81-101.
- Sprague, G.F. and Tatum, L.A. (1942). General vs specific combining ability in single crosses of corn. *J. Amer. Soc. Agron.* 34: 923-932.

(Received February 17, 1989)