

5. HORNER, E.S. 1985. Effects of selection for S_e progeny versus testcross performance in corn. In Ann. Corn and Sorghum Ind. Res. Conf. (40, 1985, Chicago). Proceedings. Washington, D.C., American Seed Trade Association p. 142-150.
6. JENSEN, S.D.; KUHN, W.E.; MCCONNELL, R.L. 1983. Combining ability studies in elite U.S. maize germplasm. In Ann. Corn and Sorghum Ind. Res. Conf. (40, 1985, Chicago). Proceedings. Washington, D.C., American Seed Trade Association p. 87-96.
7. RUSSELL, W.A.; EBERHART, S.A.; VEGA, U.S. 1973. Recurrent selection for specific combining ability for yield in two maize populations. *Crop Science* 13:257-261.
8. RUSSELL, W.A.; EBERHART, S.A. 1975. Hybrid performance of selected maize lines from reciprocal recurrent and testcross selection programs. *Crop Science* 15:1-4.
9. WALEJKO, R.N.; RUSSELL, W.A. 1977. Evaluation of recurrent selection for specific combining ability in two open-pollinated maize cultivars. *Crop Science* 17:647-651.
10. ZAMBEZI, B.I.; HORNER, E.S.; MARTIN, F.G. 1986. Inbred lines as testers for general combining ability in maize. *Crop Science* 26:908-910.

Comparison of Two Breeding Methods in Corn II. Determination of Inbreeding Depression¹

*J.A. Morera**

ABSTRACT

Examination of inbreeding and its effects contributing to genetic variation among the selfed progenies involved should help point up the changes that would occur in the selfing lines, and should be very helpful to predict progress with each of the two methods (S_e^2 progeny and testcross). To compare the two methods, bulked populations of the Syn-1, S_1 , and S_2 generations from intercrosses among selected cycle-three lines from each population and method were tested at two locations for two years. The S_2 progeny method resulted in significantly less inbreeding depression than the testcross method for grain yield of cycle-three populations, producing more vigorous lines in the S_1 and S_2 generations, whereas in the Syn-1 generation there was no significant difference between the two methods. The results suggest the possibility that both methods emphasize different types of gene action.

COMPENDIO

El examen de endogamia y los efectos que contribuyen a la variación genética entre las progenies autofecundadas involucradas, puede ayudar a delucidar los cambios que ocurren en las líneas autofecundadas; además, de predecir progreso con cada uno de los métodos (progenie autofecundada y cruce de prueba). Para comparar los dos métodos, poblaciones masales de tres generaciones (Syn-1, S_1 y S_2), provenientes de cruzamientos entre líneas avanzadas del tercer ciclo de cada población y método, fueron evaluadas en dos localidades durante dos años. El método progenie autofecundada resultó significativamente con menor pérdida de endogamia que el método cruce de prueba para rendimiento de grano, produciendo líneas más vigorosas con los sintéticos S_1 y S_2 ; mientras que el sintético 1 no mostró diferencia significativa entre métodos. Los resultados sugieren la posibilidad de que ambos métodos de selección enfatizan diferentes tipos de acción génica.

¹ Received for publication 22 July 1988.

The present work is adapted from the author's Ph.D. Thesis, supported by the German Academic Exchange Service. I wish to express my thanks to Dr. E.S. Horner, University of Florida, for his encouragement and assistance, and to the Tropical Agricultural Research and Training Center (CATIE/GTZ) for granting the leave of absence required for the program.

* Plant breeder, calles 7-9, Avenida O, Alajuela, Costa Rica, C.A.

INTRODUCTION

Inbreeding and its effect on genetic variation among the selected progenies is very helpful for understanding the changes that would occur in the selfing series. Maximum inbreeding is obtained when like gametes, A with A or a with a, unite and under such conditions the inbreeding coefficient (F) will be one because in the gene a particular character

is fixed. A random mating population, on the other hand, has a F value of zero.

Selfed progeny selection utilizes fundamentally additive and partial to complete dominance gene action. The procedure includes evaluation of S_1 or S_2 lines *per se* and selection of the highest yielding ones for intercrossing to initiate a new cycle. Testcross method selection utilizes additive gene action when the population is used as a tester (4, 6, 7, 8). It has been reported that genetic variance is, as expected, greater among selfed progenies than among testcross progenies under similar environmental conditions (1, 4).

Horner (2) pointed out that where S_2 lines were intercrossed, a generation of inbreeding increased testcross variance from 0 to 0.172. He concluded that a generation of sib-pollination prior to initiation of a new cycle would be an effective step in breeding programs. Horner *et al.* (3) compared narrow and broad base testers as well as S_2 progeny method after three cycles of selection. They concluded that the S_2 progeny method was as effective as the parental tester method for population improvement and suggested that the former places more emphasis on contributions of homozygous loci than heterozygous loci. The parental tester method produced the highest yielding random-mated (Syn-3) population, and the S_2 progeny method produced the highest yielding selfed population. Horner *et al.* (4), from two additional cycles, obtained a significant linear increase in general combining ability over cycles for all methods, but selection based on yield of S_2 progenies was less effective than the inbred tester method for improving combining ability. However, the S_2 method was just

as effective as use of the parental population as the tester. Inbreeding depression was higher in populations developed by the two testcross methods than in the S_2 progeny method. Thus, the S_2 progeny method is more effective in decreasing the frequency of recessive deleterious genes which should result in more vigorous homozygous lines. Similar results from inbreeding were obtained by Horner (5).

MATERIALS AND METHODS

Four first generation synthetics (Syn-1) were obtained by bulking equal numbers of seed from all crosses within populations and methods.

To determine the effects of selection method on yield of inbred generations, each of the four third-cycle populations was sampled by advancing 100 random S_1 lines to S_2 's by selfing. Equal numbers of seed from each population and method were bulked to form four S_1 and four S_2 bulks. These composites, along with Syn-1 bulks, were tested at two locations near Gainesville, Florida, in 1985 and 1986. Eight replications were grown each year at each location. One-row plots with 20 plants per row were planted at the rate of 36 000 plants per hectare. A split-plot design with borders between generations was used to compare the Syn-1 (SO) generation with random S_1 and S_2 bulks of the third-cycle populations. The Syn-1, S_1 , and S_2 were main plots and the four composites were subplots. The main plots were assigned to each block at random and the subplots were randomized within main plots.

Data on grain yield per plot was taken prior to harvesting. The plots were harvested by hand and

Table 1. Mean squares from the analyses of variance for grain yields of Syn-1, S_1 , and S_2 bulks from the third-cycle populations developed by the S_2 progeny and testcross methods.

Source of variation	df	Generations		
		Syn-1	S_1	S_2
Environments (E)	3	5.99**	1.82**	2.97**
Reps/E	28	0.84	0.73	0.69
Composites (C)	3	2.00**	1.55**	4.34**
Methods (M)	1	0.02	4.34**	11.38**
Populations (P)	1	3.57**	0.30	1.42*
M X P	1	2.49**	0.01	0.29
E x C	9	1.24**	0.23	0.23
E X M	3	3.28**	0.34	0.12
E X P	3	1.89**	0.25	0.43
E X (M X P)	3	0.88	0.32	0.14
Error	84	0.28	0.34	0.26
Total	127			

*, ** significant at the 0.05 and 0.01 probability levels, respectively

total number of ears and field weight to the nearest 0.1 lb were recorded. Ten good representative ears from three replications at each location were saved, dried to about 12% moisture, and shelled for dry grain determination.

Prior to statistical analysis, the yield was adjusted to full stand by multiplying the yield at harvest by the ratio of number of plants at full stand to the number of plants harvested. The factors used for each missing plant were calculated to decrease yield disadvantage that a plot with a poor stand might have compared with those plots with full stands. Finally, the field weight of each plot was converted to kilograms and adjusted for moisture and shelling percentage by multiplying the field weight by average percentage of dry grain recovery for each entry.

The average coefficient of inbreeding was calculated for each generation (Syn-1, S_1 , and S_2).

The data were analyzed as a randomized complete block design at each of the three levels of inbreeding to compare methods and populations. When significant differences were found among traits, least significant difference (LSD) was employed to separate means.

To estimate method and population effects, the sums of squares for composites were partitioned into sources of variation attributed to methods, populations, and the interaction between methods (M) and populations (P). The composites (C) and environ-

ments (E) sums of squares were similarly partitioned into E x M, E x P, and (M x P) x E sources.

RESULTS AND DISCUSSION

The S_2 progeny method was significantly better than the testcross method ($P < 0.01$) for grain yield at the S_1 and S_2 levels of inbreeding, whereas in the Syn-1 generation there was no significant difference between the two methods (Tables 1 and 2). Population B was higher yielding than Population A in the Syn-1, but the reverse occurred at the S_2 level. This indicates that less inbreeding depression occurred in Population A than in Population B (Table 2). The different response of each population resulted in a significant ($P < 0.01$) method by population interaction for the Syn-1.

Grain yields of the four selected third-cycle populations at three levels of inbreeding (Syn-1, S_1 , and S_2) show that the S_2 progeny method resulted in significantly less inbreeding depression than the testcross method (Table 2). Similar results have been reported by Horner *et al.* (3) for three cycles and by Horner *et al.* (4) for five cycles. A multiple linear regression analysis (Fig. 1) shows a close fit to linearity ($R^2 = 0.99$) for the average of both populations. Predicted grain yields of homozygous lines from the third-cycle populations were 2.4 and 1.6 mg/ha for the S_2 progeny and testcross methods, respectively (Fig. 1). Thus, for grain yield of inbred generations, the S_2 progeny method was markedly superior to the testcross method in the experiment.

Table 2. Grain yields of Syn-1, S_1 , and S_2 bulks from the third-cycle populations developed by the S_2 progeny and testcross methods. Average for two locations (1985-1986).

Method and population	Generations			Predicted ⁺ S_{∞}
	Syn-1	S_1	S_2	
	Mg/ha			
S_2 progeny method				
A (C3)	6.43	4.56	3.52	2.59
B (C3)	6.48	4.44	3.22	2.20
Mean	6.45	4.50	3.37	2.40
Testcross method				
A (C3)	6.17	4.17	2.83	1.84
B (C3)	6.78	4.09	2.72	1.37
Mean	6.47	4.13	2.77	1.60
L.S.D.	0.26	0.29	0.25	
Means (0.05)				

+ Yield of 100% homozygous lines predicted by linear regression.

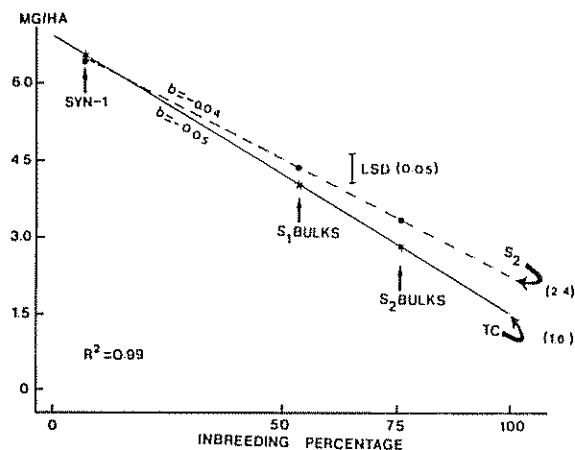


Fig. 1. Inbreeding depression in cycle 3 populations developed by S_2 progeny (S_2) and testcross (TC) methods. Mean of two populations and two years for each method. Values at right are predicted yield of homozygous lines for the two methods.

LITERATURE CITED

- DARRAH, I. L.; EBERHART, S. A.; PENNY, L. H. 1978. Six years of maize selection in 'Kitale synthetic II', 'Ecuador 573', and 'Kitale composite A' using methods of the comprehensive breeding system. *Euphytica* 27:191-204.
- HORNER, E. S. 1968. Effect of a generation of inbreeding on genetic variation in corn (*Zea mays* L.) as related to recurrent selection procedures. *Crop Science* 8:32-35.
- HORNER, E. S.; CHAPMAN, W. H.; LUTRICK, M. C.; LUNDY, H. W. 1969. Comparison of selection based on yield of topcross progenies and of S_2 progenies in maize (*Zea mays* L.). *Crop Science* 9:539-543.
- HORNER, E. S.; LUNDY, H. W.; LUTRICK, M. C.; CHAPMAN, W. H. 1973. Comparison of three methods of recurrent selection in maize. *Crop Science* 13:485-489.
- HORNER, E. S. 1985. Effects of selection for S_2 progeny versus testcross performance in corn. In *Ann. Corn and Sorghum Ind. Res. Conf* (40., 1985, Chicago). Proceedings. Washington, D.C., American Seed Trade Association p. 87-96.
- PENNY, L. H.; RUSSELL, W. A.; SPRAGUE, G. F. 1962. Types of gene action in yield heterosis in maize. *Crop Science* 2:341-344.
- RUSSELL, W. A.; EBERHART, S. A.; VEGA, U. A. 1973. Recurrent selection for specific combining ability for yield in two maize populations. *Crop Science* 13:257-261.
- SPRAGUE, G. F.; RUSSELL, W. A.; PENNY, L. H. 1959. Recurrent selection for specific combining ability and type of gene action involved in yield heterosis in corn. *Agronomy Journal* 51:392-394.

This was expected because the S_2 progeny method places more emphasis on contributions of homozygous loci than heterozygous loci, while the reverse is true for the testcross method. The two breeding methods apparently emphasize different types of gene action, as would be expected from genetic theory (4, 7, 8). The S_2 progeny method places more emphasis on the contribution of alleles in the homozygous state, which resulted in appreciably higher-yielding inbred lines in the third cycle than were obtained with the inbred tester method. The inbred tester method, on the other hand, emphasizes the contribution of heterozygous loci, resulting in a higher inbreeding depression than was obtained with the S_2 progeny method. These results suggest the possibility of overdominant gene action at some loci.