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Criteria for Developing Second-cycle Hybrids in Maize

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Abstract: Recycling of F1 maize hybrid Lorena was conducted in two breeding cycles. The breeding scheme was based on inbred line method for improving yielding performance of lines *per se*. The line development was based on a pedigree selection scheme with selfing and evaluation under favourable field conditions. Early evaluation included honeycomb designs and wide spacing. After two cycles of recycling, heterosis and heterobeltiosis level was found very low or negative and inbred line yielding performance *per se* was high reaching the original hybrid's yield. This indicated excessive exploitation of favourable additive gene action, which leads to homozygote advantage. Final crosses were similar or sometimes better than original hybrid. Several criteria were used for the breeding procedure. The choice of starting material was based on inbreeding depression, general combining ability and specific combining ability estimation conducted previously. The breeding procedure was based on additive gene action. Breeding scheme was based on a new approach of the inbred line method on cross-fertilized species and the final target was focused on maximizing yielding performance and not heterosis. Evaluation during early stages was based in favourable experimental conditions, incorporating honeycomb field designs.

Key words: Second-cycle hybrids, maize, recycling, criteria

INTRODUCTION

Maize breeders lead their breeding programs to an excessive exploitation of heterosis, which is rendered on the function of alleles showing dominance effects (Smith, 1984). According to Kearsey and Pooni (1992), heterosis is caused by dispersed genes showing mainly directional dominance and not by heterozygote superiority or complementary epistasis. On the other hand, additive gene action is of great importance, because this kind of action insures heritable and stable performance (Fasoulas, 1993; Ipsilandis and Koutsika-Sotiriou, 2000) and may insure high yields for crosses developed under genetically narrow-based crossing programs (Ipsilandis and Koutsika-Sotiriou, 1997; 2000). Genter and Alexander (1966) stated that, if the performance of S1 lines depends mainly on additive effects, then the yield of their crosses would be proportional to their yielding performance *per se* and thus, it is possible, that selection practiced for improving line performance per se, leads to the accumulation of favourable additive genes. Ipsilandis and Koutsika-Sotiriou (1997) proposed S1 selection for productivity of lines *per se* in low-stress conditions during the very early stages.

Maize hybrid recycling was proposed by many researchers, by means of developing second-cycle inbred lines derived from elite F2s of commercial hybrids (Toledo *et al*., 1984; Hallauer, 1990; Koutsika *et al*., 1990; Ipsilandis, 1996; Ipsilandis and Koutsika-Sotiriou, 2000). Tokatlidis *et al*. (2005) showed that second-cycle maize hybrids developed from honeycomb breeding schemes, usually are less density dependent than original hybrid due to their improved yield potential per plant resulting in higher grain yield at lower plant densities. Koutsika-Sotiriou (1999), proposed three criteria for evaluating commercial maize hybrids as starting materials for developing second cycle inbred lines: inbreeding depression (ID), general combining ability (GCA) and specific combining ability (SCA). Furthermore, Fasoula and Fasoula (2000; 2002) proposed a combined criterion for whole-genome phenotypic evaluation under honeycomb breeding schemes, concerning (a) genes that control yield potential per plant, (b) genes that confer tolerance to biotic and abiotic stresses and (c) genes that control responsiveness to inputs.

The aim of this study was to develop new maize hybrids after two cycles of recycling based on practical selection criteria and to evaluate the recycled inbred lines for yielding performance *per se*.

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MATERIALS AND METHODS

This study was based on hybrid reconstruction techniques described by Koutsika-Sotiriou *et al.* (1990). Recombinant lines in S5 and S6 generation, developed from two cycles of combined Half-sib/S1 evaluation on widely-spaced plants in the direction of high yielding *per se*, were used. During the first cycle (years 1987-1995) recombinant lines were developed from the F2 generation of F1 commercial single-cross maize hybrid Lorena (PR3183), according to the procedure described by Ipsilandis (1996), Ipsilandis and Koutsika-Sotiriou (2000). General combining ability (GCA) estimation was based on the formula given by Falconer (1989). The recombinant lines of second cycle were developed from the F2 generations of four crosses derived from the first cycle of hybrid reconstruction. Two of them involved S5 X S5 inbreds and the other two S5 X FR (Free-release) inbreds. Each F2 consisted of 200 plants, shown in a R0 honeycomb design (Fasoulas, 1988) with 1.5 m plant to plant distance, for better expression and evaluation of individual plants (Ipsilandis and Koutsika-Sotiriou, 2000). The S-line development was based on a pedigree selection scheme, where only the best 10% of the plants were selected after *per se* evaluation in a moving block design (Fasoulas, 1985) and their selfed progenies were used to produce the next generation until the S5 and S6. The spacing between rows was 1 m and between plants on the row was 0.5 m. In early stages S1 and HS evaluation was conducted to determine yielding performance and inbreeding depression, as described by Ipsilandis (1996); Ipsilandis and Koutsika-Sotiriou (2000). Estimation of inbreeding depression was based on the formula given by Goulas and Lonnquist (1976).

The four crosses selected after the first cycle of hybrid reconstruction were namely: D-17 X C-22, D-17 X A-27, D-17 X Va26 and A-27 X Va26 (Ipsilandis and Koutsika-Sotiriou, 2000; Vafias and Ipsilandis, 2005). In that way they formed four groups of progenies (A, B, C and D). The coding of the new lines developed was similar to the one used by Ipsilandis and Koutsika-Sotiriou (2000), Vafias and Ipsilandis (2005). Only the letter of the group was added in front of the new numbers (A,B,C,D). Inbreeding depression estimation was based in S1/HS evaluation by the formula given by Goulas and Lonnquist (1976) in the same way as in the first cycle. The S-line development was based on pedigree selection scheme, where only the best 10% of the plants were selected after *per se* evaluation in a moving block design (Fasoulas, 1985) and their selfed progenies were used to produce the next generation until the S5 and S6. The combining ability tests of inbred lines derived from the four recycled crosses, consisted of crosses between best S5 inbred lines. The second cycle lasted from year 1996 to 2003, involving selfings for one year in Technological Education Institute farm of Florina to produce S6 generation. The total cycle was established in Technological Education Institute farm of Larissa.

Evaluation of crosses was conducted in Technological Education Institute farm of Larissa, Greece, in four different but adjacent fields, during year 2003. Evaluation of S6 lines was conducted in a separate field. The tester for hybrids was F1 hybrid Costanza and for lines the inbred line B73. Hybrid Costanza was tested in common experiments with hybrids Lorena and Dona during 1999, in order to get relative yielding performance for hybrid testers. Relative performance was adjusted to the yields of Lorena and B73 found by Ipsilandis and Koutsika-Sotiriou (2000). The additional evaluation of 2003 of the testers Costanza and B73 revealed a different yield relation between them because hybrid Costanza showed slightly lower yielding performance when compared to 1999 (B73 was found at the same level), for this, newer relation (and relative yielding performance) was used at the final stage of evaluation. The experimental design was a Randomized Complete Block (RCB) with 4 replications for all field trials. In all yield tests the experimental plot consisted of two 5 m long rows, spaced 80 cm apart. All plots contained 50 plants, i.e., 25 plants/row giving a density of 6.25 plants m^{-2}. All plants were grown using conventional fertilizer applications and weed/pest control in order to promote high productivity. Grain yields from each plot were measured after adjusting to 15.5% grain moisture. The RCB analysis was based on the null hypothesis by means of an analysis of variance at the 0.05 probability level (Gomez and Gomez, 1984). Middle-parent Heterosis and Heterobeltiosis to best parent in cross for all types of crosses were computed by formulas proposed by Koutsika-Sotiriou and Bos (1996) and applied by Ipsilandis and Koutsika-Sotiriou (2000).

RESULTS

As shown in Table 1, there were a few S5 crosses that over yielded the original hybrid Lorena, especially when S5 lines were crossed to free-release (FR) inbred lines of different pedigree. Crosses D-17 X C-22 (86% in relation to Costanza) and D-17 X A-27 (69-86% in relation to Costanza) were promising materials derived from high yielding lines, even though the second cross showed lower yielding performance and also crosses to FR lines yielded over 95% in relation to Costanza. The best inbred line was D-17 (60% in relation to Costanza and 280% in

Table 1: First cycle of recycling Lorena (PR3183)

S4XS4, S5XS5 and S5XFR crosses					
Hybrids	Yield (%) Lorena	Yield (%) Costanza	Yield (%) B73	Middle-Parent heterosis	Heterobeltiosis to best parent
D-17 X C-22 S4	100	86	400	60	43
D-17 X A-27 S4	80	69	320	37	14
D-17 X A-27 S5	100	86	400	60	43
D-17 X C-22 S5	100	86	400	60	43
C-22 X Va26	117	101	468	175	113
A-27 X Va26	112	97	448	164	104
D-17 X Va26	110	95	440	120	57
Dona	118	102	472	-	-
Costanza	116	100	464	-	-
Lorena	100	86	400	-	-
S6 First cycle lines					
Inbred lines S6	Yield (%) Lorena	Yield (%) Costanza	Yield (%) B73	Inbreeding depression	Mean GCA
D-17	70	60	280	10	1645
A-8	65	56	260	-75	-1213
C-35	65	56	260	50	-
C-33	60	52	240	25	-2384
A-27	55	47	220	-25	-1093
C-22	55	47	220	65	475
Va26	30	26	120	-	722
B73	25	22	100	-	-2110

Lorena 100= 14300+/-840 kg ha^{-1}

Table 2: Second cycle of recycling Lorena (PR3183)

Hybrids	Yield (%) B73	Yield (%) Costanza	Yield (%) Lorena	MP heterosis	Heterobeltiosis BP	Lines	Inbreeding depression	Yield (%) B73	Yield (%) Costanza	Yield (%) Lorena
Costanza*	410	100	116	-	-	B73*	-	100	24	28
A-1 X A-2	400	98	113	10	0	A-1	-50	400	98	113
A-1 X A-6	400	98	113	18	0	A-2	-18	330	80	93
A-1 X A-4	360	88	102	4	-10	A-3	-55	305	74	86
A-1 X A-5	380	93	108	11	-5	A-4	-	290	71	82
A-1 X A-3	360	88	102	2	-10	A-5	-	285	70	81
A-2 X A-6	360	88	102	18	9	A-6	0	280	68	79
A-2 X A-4	345	84	98	11	5					
A-4 X A-6	320	78	91	12	10					
B-1 X B-2	390	95	110	8	0	B-1	-55	390	95	110
B-1 X B-6	400	98	113	19	3	B-2	-36	335	82	95
B-1 X B-4	380	93	108	11	-3	B-3	-	310	76	88
B-1 X B-5	360	88	102	6	-8	B-4	-	295	72	83
B-1 X B-3	350	85	99	0	-10	B-5	-	290	71	82
B-2 X B-6	370	90	105	20	10	B-6	10	280	68	79
B-2 X B-4	350	85	99	11	4					
B-4 X B-6	325	79	92	13	10					
C-1 X C-2	400	98	113	8	0	C-1	-40	400	98	113
C-1 X C-6	400	98	113	16	0	C-2	-14	340	83	96
C-1 X C-4	375	91	106	6	-6	C-3	-	315	77	89
C-1 X C-5	370	90	105	6	-8	C-4	-	305	74	86
C-1 X C-3	370	90	105	3	-8	C-5	-	300	73	85
C-2 X C-6	350	85	99	11	3	C-6	12	290	71	82
C-2 X C-4	350	85	99	9	3					
C-4 X C-6	325	79	92	9	7					
D-1 X D-2	400	98	113	9	1	D-1	-33	395	96	112
D-1 X D-6	410	100	116	21	4	D-2	-11	340	83	96
D-1 X D-4	380	93	108	9	-4	D-3	-	315	77	89
D-1 X D-5	370	90	105	8	-6	D-4	-	300	73	85
D-1 X D-3	370	90	105	4	-6	D-5	-	290	71	82
D-2 X D-6	370	90	105	19	9	D-6	-	280	68	79
D-2 X D-4	355	87	100	11	4					
D-4 X D-6	330	80	93	14	10					

Yield values >11% are significant at $p<0.05$ (*) B73 and Costanza were compared in new experiments, A = D-17 X C-22, B = D-17 X A-27, C = D-17 X Va26, D = A-27 X Va26 relation to B73). Middle-parent heterosis was low when lines of common pedigree were crossed (usually around 60%). Heterobeltiosis to best parent was found also low (usually 43%). Inbreeding depression was found also low and sometimes negative.

In Table 2, after the second cycle of recycling the original hybrid Lorena, most of the selected lines were high yielding (280 to 400% in relation to B73 and up to 98% in relation to Costanza). Sometimes these lines over yielded original hybrid Lorena but almost within non-significance levels. The crosses between these lines were interesting since many of them over yielded original hybrid Lorena, but heterosis was very low and heterobeltiosis to best parent was even lower and usually negative, especially when the best recycled line was involved. Lower yielding lines *per se* showed a good yielding performance in their crosses accompanied by heterosis, but heterobeltiosis to best parent was found very low.

DISCUSSION

Two cycles of recycling resulted in high yielding maize crosses and in elite inbred lines that serve as hybrid parents. In the first cycle the inbred lines derived from the F2 of commercial hybrid Lorena, were high yielding (65-70% of he original hybrid and 56-60% of hybrid Costanza). This was attributed to favourable additive gene action (Ipsilandis and Koutsika-Sotiriou, 2000). Inbreeding depression was found low and this was considered an additional evidence of additive gene action (Fasoulas, 1988; Genter, 1967). In such conditions, yield distributions are biased according to the load of deleterious genes (Fasoulas, 1988, 1993; Ipsilandis and Koutsika-Sotiriou, 1997). Reversely, when departure from normality is apparent, this indicates deleterious gene action. Mean general combining ability (GCA) exhibited by these lines was not always high or positive. Additionally, middle-parent heterosis was low and heterobeltiosis to best parent was even lower. These findings were not problems since the crosses between high yielding S4 and S5 lines exhibited good yielding performance and this was more apparent in crosses between S5 and Free-release inbred lines of different pedigree as reported also by Vafias and Ipsilandis (2005).

Inbreeding depression (ID), general combining ability (GCA) and specific combining ability (SCA) estimation for seven commercial F1 single maize hybrids, were recorded as criteria for hybrid reconstruction (Koutsika-Sotiriou, 1999). Low inbreeding depression, positive general combining ability and negative specific combining ability were found to be criteria for best promising starting materials (Koutsika-Sotiriou, 1999; Koutsika-Sotiriou and Karagounis, 2005). Starting material of present study Lorena, complies with these criteria.

The second cycle of recycling original hybrid resulted in high yielding crosses. All these crosses reached the yielding performance of the original hybrid Lorena and 8 of them over yielded original hybrid. Additionally, 18 crosses reached the yielding performance of tester Costanza. The final lines after two cycles of recycling were extremely high yielding since they over yielded the tester B73 (even four times). Four of them reached original hybrid's yielding performance, exhibiting inbreeding superiority. Inbred lines that incorporate favourable genes in an integrated genome are able to reach hybrid's yielding performance (Genter 1967; Toledo *et al*., 1984; Fasoulas, 1993). In such conditions middle-parent heterosis and heterobeltiosis to best parent was found very low or negative because of excessive exploitation of favourable additive gene action (Fasoulas, 1988; Vafias and Ipsilandis, 2005; Ipsilandis *et al*., 2005). It is now clear that low heterosis or heterobeltiosis may not be a problem to maize breeders. Genter (1973) was the first who stated that breeders' aim must be the maximization of yielding performance and not maximization of heterosis. Present study and previously conducted studies (Ipsilandis and Koutsika-Sotiriou, 2000; Vafias and Ipsilandis, 2005) showed that removal of deleterious genes and simultaneous accumulation of favourable additive genes, may lead to reduced heterozygosity and heterosis accompanied by high yielding performance (Genter, 1967; Fasoulas, 1988). Ipsilandis (1996) and Ipsilandis and Koutsika-Sotiriou (2000), reported that low inbreeding depression and additive gene action in segregating genetic materials may lead to development of elite second-cycle maize inbred lines and consequently to high yielding crosses (recycled hybrids or completely new hybrids with lower level of heterozygosity). It is expected, high yielding inbred lines used in crosses to express favorable additive gene action when considering yielding performance both per se or in crosses where the level of heterozygosity is low (Fasoulas, 1993; Ipsilandis, 1996; Fasoula and Fasoula, 1997; Ipsilandis and Koutsika-Sotiriou, 1997, 2000). Another consequence of this fact is that hybrids formed by crossing high yielding inbred lines may depend a portion of their vigor on favorable additive gene action, since such kind of loci may be alike in the two parents especially when they derived from common pedigree (Fasoulas, 1993; Ipsilandis, 1996; Ipsilandis and Koutsika-Sotiriou, 1997, 2000; Ipsilandis and Vafias, 1998). Genter (1967) also reported that gene action may be completely additive or may balance between partial to complete dominance, resulting in homozygous individuals with yielding performance similar to that of hybrids (heterozygous individuals). In that way, breeding inbred lines for *per se* performance may be an effective procedure. This hypothesis results to a new usage of the inbred line method: breeding of cross-fertilized species. Two elite lines may combine to a cross with high and stable yield (Genter and Alexander, 1966). Genter and Alexander (1966) stated that, if the performance of S1 lines depends mainly on additive effects, then the yield of their crosses would be proportional (positively related) to their yielding performance *per se* and thus it is possible, selection practiced for improving line performance *per se*, to lead in accumulation of favourable additive genes.

Low inbreeding depression found in our study and fixation of additive gene action may lead to a new breeding approach with final target the development of inbred lines as the final commercial products of the breeding procedure. Inbred lines exhibiting inbreeding vigor may be used in crosses, or to replace hybrids in the farmer's field. Fehr (1987) consider as the final breeder's target, the production of new varieties exhibiting high and stable yielding performance. Fasoulas (1988, 1993) categorized the variety production to five distinct categories according their genetic background, but he also stated that the development of inbred lines may unify all the different procedures used. The present study is in agreement with those statements, but the stability of the performance of elite lines must be tested in specific experiments across locations and years.

Concluding, the present study was based on several criteria. The choice of starting material was based on inbreeding depression, general combining ability and specific combining ability estimation conducted previously (Koutsika-Sotiriou, 1999; Koutsika-Sotiriou and Karagounis, 2005). The breeding procedure was based on additive gene exploitation (Genter, 1967; Fasoulas, 1988, 1993; Ipsilandis *et al*., 2005). The breeding scheme was based on a new approach of the inbred line method (Ipsilandis, 1996; Ipsilandis and Koutsika-Sotiriou, 2000; Vafias and Ipsilandis, 2005). The final target was focused on maximizing yielding performance and not heterosis (Genter, 1973; Fasoulas, 1993). Evaluation during early stages was based in favourable experimental conditions, incorporating honeycomb designs and wide interplant spacing (Fasoulas, 1988, 1993). Combined criterion proposed by Fasoula and Fasoula (2000, 2002) for more reliable phenotypic evaluation, improves honeycomb breeding schemes by assaying genes that control yield potential per plant, genes that confer tolerance to biotic and abiotic stresses and genes that control responsiveness to inputs. Additionally, honeycomb breeding schemes result in the development of density independent second-cycle hybrids (Tokatlidis *et al*., 2005). In present study for hybrid recycling, only field yielding performance was evaluated to depict the efficacy of the method used. Combined criterion was not used because of the conventional experimentation during final stages. The final result of development high yielding inbred lines, showed an alternative way in breeding of cross-fertilized species.

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