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Breeding for Homozygotic Superiority and Stability in Maize without Losing Combining Ability

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Abstract: A review study on maize hybrid and inbred line productivity and stability, in an effort to overcome stagnation by developing more efficient breeding strategies. Data presented here, refer to maize hybrid and inbred line yields, under high and low plant populations, which depict the need for incorporation of favourable additive gene action in the genetic materials, under pedigree line selection schemes evaluating *per se* performance. Additionally, low populations during the first stages of selection, contribute to more reliable evaluation of favourable genotypes. Data reveal that inbred lines are capable to reach hybrid performance and consequently, replace single hybrids as the end-products for farmer use. As far as the yielding capacity of inbred parents improves, the less the yield in F1 is favored by heterozygosity. Other products, such as three-way crosses with lower level of heterozygosity, may be more efficient and stable than single hybrids and more readily developed. These products depend their productivity on additive gene action. Stability and uniformity of performance of three-way crosses is depended on high and stable inbred line performance. In general, these breeding strategies may lead to more stable end-products, density independent and with satisfactory yielding performance.

Key words: Yield performance, hybrids, inbred lines, inbreeding depression

INTRODUCTION

Maize breeders are focused in achieving high and stable yielding performance of hybrids in the field^[1,2]. Heterosis is a dramatic phenomenon that is realised during hybridization and was utilised by maize breeders to improve productivity^[3]. Maize hybrids was a revolutionary material to improve productivity and replaced maize populations that was cultivated 100 years ago^[4-6]. Double hybrids was the first step for commercial utilization of heterosis, which resulted in annual gain of productivity of 65 kg ha⁻¹, but later, single hybrids enlarged annual gain to 110 kg ha⁻¹^[7,8]. Modern maize hybrids, exhibit higher and stable grain yield productivity across different environments^[8], which resulted indirectly by improving a range of traits associated with tolerance to various biotic and abiotic stresses and by improving the efficiency of capture and use of resources^[2,9-12]. Tollenaar^[13] concluded that the plant density might be a major stress to older hybrids with minor impact to newer ones. Additionally, differences in grain yield between older and newer maize

single hybrids were shown to be a function of plant population density^[14] and as a result of replacement of older inbred lines with newer ones, which incorporate desirable characteristics contributing to stress tolerance under various environmental conditions^[11]. Fasoula and Fasoula^[15,16] distinguished three components of crop yield potential: the potential yield per plant in the absence of competition, the tolerance to stresses and the responsiveness to inputs. Starting genetic material (source germplasm), the final target for high and stable yielding performance and the breeding procedure, are defined by the breeder. Source germplasm used by maize breeders includes primarily F2 (recombinant crosses), backcross and synthetic populations^[17]. Jenkins^[18] reported increased use of F2 and backcross populations since 1948 for second-cycle inbred development programmes, with a corresponding rapid decline in use of open pollinated cultivars. Ipsilandis and Koutsika-Sotiriou^[9] suggested F2 generation of a commercial hybrid as starting genetic material, for two reasons: a) to shorten the breeding program by

avoiding population improvement, b) exploitation of favourable additive gene action.

The following discussion is a review on the breeding procedure in maize. It emphasizes on the homozygotic superiority of elite inbred lines exploiting favourable additive gene action. As a consequence, second-cycle hybrids may have a lower level of heterozygosity, expressing additive gene action. Inbred lines used as parents of hybrids, must accomplish a number of criteria, in order to express homozygotic superiority without losing combining ability.

BREEDING PROCEDURE

The breeding methods: A successful breeding program in developing new maize hybrids, depends not only on the germplasm but also on the procedure for developing inbred parents and consequently new promising crosses^[19]. Maize breeders excessively utilised heterosis, which is rendered on the function of alleles showing dominance effects^[20,21]. According to Kearsy and Pooni^[22], 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^[19,23,24] and may insure high yields for crosses developed under genetically narrow-based crossing programs^[19,25]. A maize breeder has to balance between the three main goals of breeding (productivity, uniformity, stability) and the cost of hybrid seed production because of the low productivity of inbred parents as well as the need of separate plantings under isolation^[1]. The practical difficulties associated with the low productivity of inbred lines can be overcome by three different approaches:

- The use of 3-way or 4-way crosses^[1,6,21].
- The use of the backcross method for step-by-step improvement^[1,21].
- The improvement of productivity *per se* of modern inbred lines that serve as parents in crosses^[19,26]. The most common practice involves family selection schemes^[1,6,23] aiming to replace deleterious genes by favourable (additive) alleles. Fasoulas^[23] proposed honeycomb selection designs to insure comparable conditions for all entries and enhance the effectiveness of selection under favourable conditions, in absence of competition.

Combined S1/HS selection, was proposed to improve both productivity *per se* and combining ability^[19,27,28].

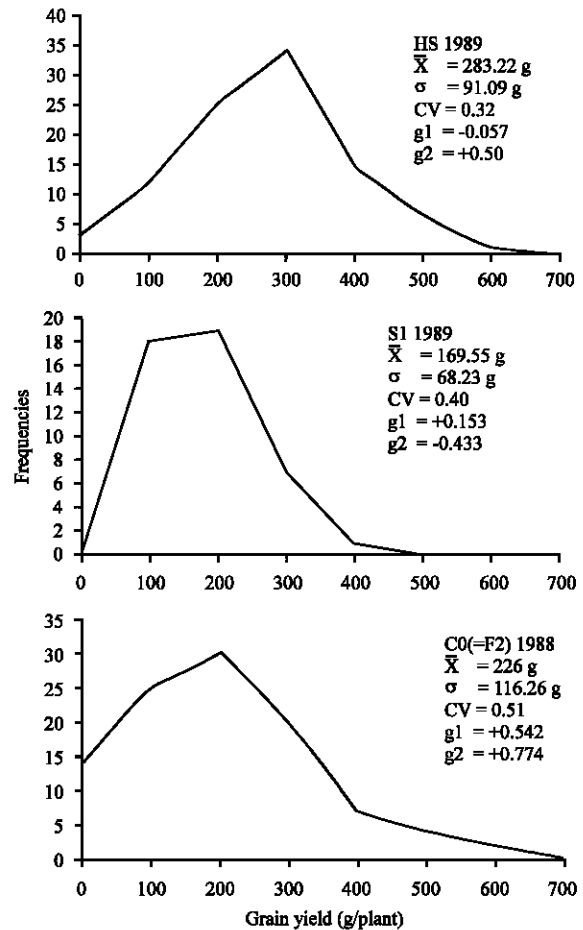


Fig. 1: Single plant grain yield frequency distributions for F2 and S1/HS progenies (hybrid PR3183)^[25].

Mass selection is not a common practice in modern maize breeding. It was used in the past for population improvement in segregating materials, but recurrent selection schemes replaced population improvement by mass selection of genotypes^[29,30].

Yield frequency distribution: When evaluating F2 generation and S1 progenies' distributions, departure from normality is apparent (Fig. 1), indicating deleterious gene action^[23,25,31]. Strong positive skewness, indicates the presence of inferior genotypes exhibiting inbreeding depression, which is absent in Half-sib (HS) yield distribution^[23,31]. The General Combining Ability (GCA) of HS families (Fig. 2), showed a normal distribution^[19]. The percentage of deleterious genes (equivalent to inbreeding depression percentage) was estimated to be 40%, according to Fasoulas^[23,31]. The inbreeding depression distribution (Fig. 2) showed that the most common values were about 25-30%, as many S1 families have been

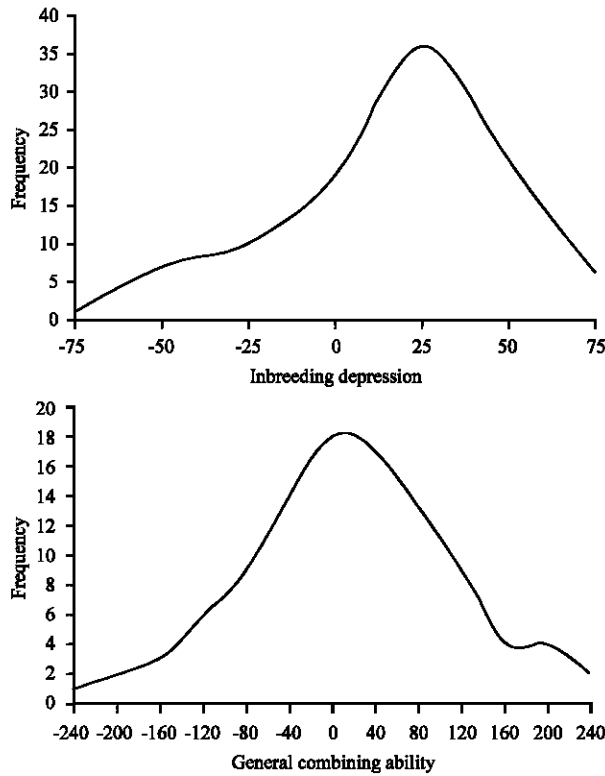


Fig. 2: The inbreeding depression frequency distribution of S1 families and the General Combining Ability (GCA) frequency distribution of HS families (hybrid PR3183)^[19]

out yielded by the corresponding HS families at the same percentage. The combining ability for some HS families was high and their yielding performance was greater than the original F1 hybrid. The inbreeding depression distribution (Fig. 2) showed that a few S1 families had negative inbreeding depression, because they out yielded the corresponding HS families. These indications revealed the importance of favourable additive gene action, which is present in segregating genetic materials with a lower level of heterozygosity than the F1 single-cross hybrid^[23,32,33]. According to the above mentioned data (Fig. 1 and 2) inbreeding depression and (general) combining ability are two different approaches of the same phenomenon which is caused by the presence of deleterious genes that are masked when crossing is taking place^[19,23,31].

INBRED LINES

The inbred lines as parents: Hybrid development, involves crossing between elite inbred lines, resulting to

Table 1: Relative yield (%) to Lorena and to inbred line B73, inbreeding depression and mean General Combining Ability (GCA) for lines used as hybrid parents^[19]

Inbred line	Yield % Lorena	Yield % B73	Inbreeding depression %	Mean general combining ability
Freely available inbred lines				
5C	55	220	-	+638
P-6	40	160	-	-
B84	30	120	-	+1391
Va26	30	120	-	+722
Va22	25	100	-	-1220
B73	25	100	-	-2110
Recombinant lines				
D-17	70	280	+10	+1645
A-29	65	260	+25	-
A-8	65	260	-75	-1213
C-35	65	260	+50	-
C-33	60	240	+25	-2384
A-27	55	220	-25	-1093
C-22	55	220	+65	+475
D-1	50	200	+10	-
C-10	50	200	+75	-
B-24	45	180	-10	-
D-30	40	160	+35	-
C-27	31	125	+30	-
D-27	30	120	+35	-
B73	25	100	-	-

Lorena 100 = 14300' 840 Kg ha⁻¹

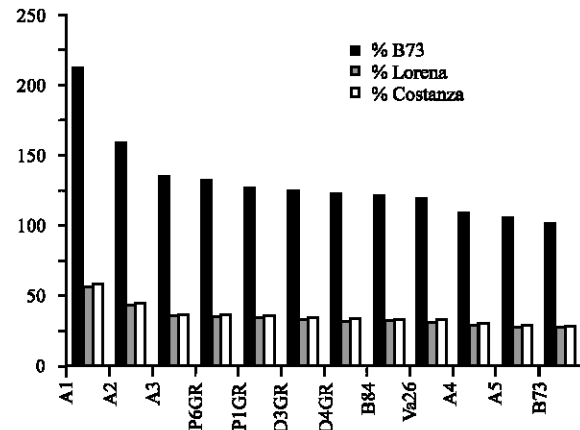


Fig. 3: The inbred lines used in second-cycle crosses, relative yield as percentage: of B73 (%B73), F1 hybrid Lorena (%Lorena) and F1 hybrid Costanza^[34]

an increasing productivity by exploiting heterosis. Elite lines used in crosses are shown in Fig. 3^[34].

Considering crossing between recombinant lines of common pedigree, general combining ability is of small importance, since heterosis was found to be low and heterobeltiosis even lower (Table 1 and 2)^[19]. These crosses depend their yielding performance on favourable additive gene effects, common in the two parents and consequently the second-cycle hybrids between them must be in a lower level of heterozygosity compared to the

Table 2: Relative yield (%) to Lorena, middle-parent heterosis (%), heterobeltiosis to best parent and to second parent (%) for crosses between S4, S5 recombinant lines and between recombinant lines and freely available inbred lines^[19]

Crosses	Yield %		Heterobeltiosis to best parent	Heterobeltiosis to 2nd parent
	Lorena	Middle-parent Heterosis(%)		
Crosses between S4 recombinant lines				
Lorena	100	-	-	-
D-17 X C-22	100	+60	+43	+82
D-17 X C-33	88	+36	+26	+46
D-17 X C-35	81	+20	+15	+25
D-17 X A-27	80	+37	+14	+60
A-27 X B-29	80	-	+43	-
A-27 X C-10	77	+47	+40	+54
A-27 X C-33	72	+26	+31	+20
A-27 X C-35	70	+18	+27	+8
D-17 X D-1	65	+12	-7	+30
A-27 X A-8	50	-16	-9	-23
A-27 X C-22	47	-15	-15	-15
Crosses between S5 recombinant lines				
Lorena	100	-	-	-
D-17 X A-27	100	+60	+43	+82
D-17 X C-22	100	+60	+43	+82
D-17 X C-33	99	+52	+41	+65
D-17 X A-8	89	+32	+27	+37
D-17 X D-27	89	+78	+27	+197
D-17 X C-27	83	+66	+19	+177
D-17 X B-24	82	+52	+17	+87
D-17 X D-5	80	-	+14	-
D-17 X D-30	77	+40	+10	+92
A-27 X A-8	70	+17	+7	+27
Crosses between unrelated lines				
Dona	118	-	-	-
C-22 X Va26	117	+175	+113	+290
C-22 X 5C	113	+105	+105	+105
C-22 X B84	112	+164	+104	+273
A-27 X Va26	112	+164	+104	+273
C-33 X P-6	111	+122	+85	+177
D-17 X Va26	110	+120	+57	+267
C-22 X P-6	109	+129	+98	+172
C-22 X Va22	106	+165	+93	+324
A-27 X 5C	105	+91	+91	+91
D-17 X 5C	100	+60	+43	+82
Lorena	100	-	-	-
C-33 X Va22	98	+131	+63	+292
D-17 X B84	98	+96	+40	+227
D-17 X Va22	92	+94	+31	+268
D-17 X P-6	92	+67	+31	+130
C-22 X B73	69	+72	+25	+176
A-27 X B73	59	+47	+7	+136
A-8 X B73	44	-2	-32	+76
D-17 X B73	40	-16	-43	+60

original hybrid^[11,19,23,25,35,36]. Genter and Alexander^[33] 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. Sotiriou *et al.*^[37] concluded that in such cases the genetic background consist mainly of additive or partially dominant alleles. When crossing unrelated inbred lines, middle-parent heterosis can be more easily realized in comparison to crossing between recombinant lines of common^[19].

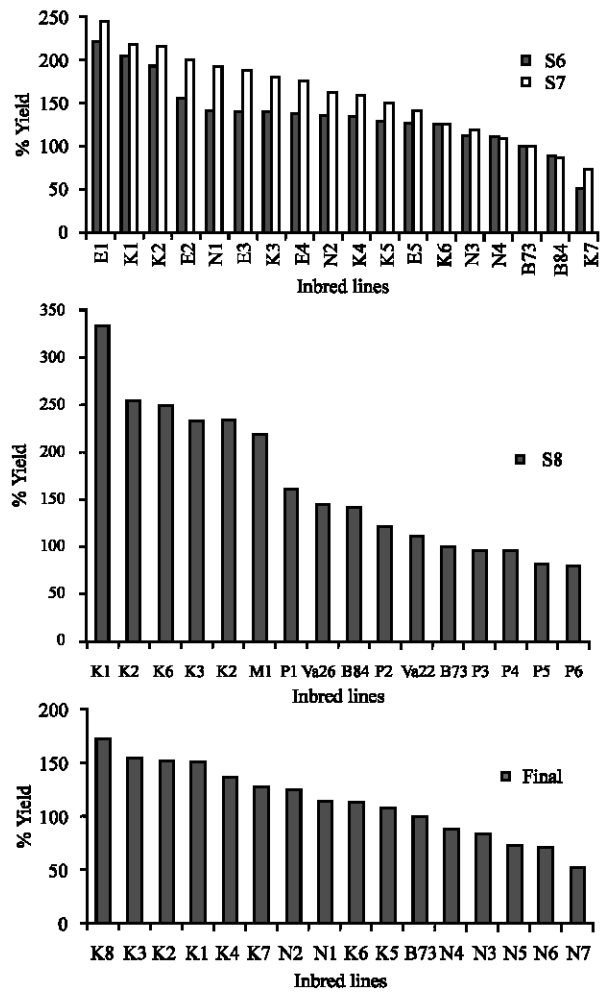


Fig. 4: Experimental inbred lines' (S6, S7, S8 and final stage) yields %, compared to B73 yield (=100), derived from five different breeding programs (unpublished data adapted from C.G. Ipsilandis, *et al.*)

Yielding performance *per se* of inbred lines: Inbred line stagnation for productivity and stability, is reflected in two consequences: (a) the *per se* productivity of lines remained below 50% in comparison to single crosses for 50 years and (b) the inability to predict hybrid performance^[38]. Breeding of a maize source population is considered to be an effective way to enhance the development of superior inbred lines^[39] and proper germplasm determines the success of selection for genetic improvement^[40]. Seeking for elite lines, Ipsilandis and Koutsika-Sotiriou^[19,25] started with S1 families with a mean yield corresponding to 32% of the original hybrid (Lorena, PR3183) and improved the mean yield to 46% for S5 or 42% for S6. The best S5 recombinant lines yielded from 50 to 70% the yield of the original single-cross hybrid

(Lorena), while the B73 inbred line yielded only 25% (Table 1). These inbred lines were developed from the F2 generation of PR3183 via controlled selfing and combined S1/HS selection without any previous population improvement^[19,25,28]. The recombinant line D-17 was a high yielding line *per se* (70% of Lorena) due to the accumulation of favourable additive genes^[19,31]. Also from diallel crosses trials (Table 1), it is clearly seen that D-17 contributes the most in GCA (+1645) because of its yielding performance *per se*, compared to other lines of lower yielding performance. Papadopoulou^[41], Evgenidis *et al.*^[42] and Evgenidis^[43], reported increased *per se* yielding performance, as a result of previous population improvement based on honeycomb breeding method principles^[15,16], with the best promising inbreds reaching 70-90% of original hybrid PR3183. Vafias and Ipsilandis^[34] and C.G. Ipsilandis *et al.* (unpublished data from common experiments), found that recombinant line yielding performance *per se* could overcome B73's yield by two or three times (Fig. 3 and 4), indicating the concentration of favourable additive genes that contribute to high line performance.

Fasoulas^[38] and Fasoula and Fasoula^[44], reported the PC criterion for ranking inbred lines and depicted that on the basis of PVC, lines derived from the F2 are superior to lines derived following previous population improvement. Additionally, Fasoula and Fasoula^[15,16], proposed a combined criterion for whole-genome phenotypic evaluation 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.

MAIZE HYBRIDS

Yielding performance of maize hybrids: Maize hybrids are the final products of a breeding program. Ipsilandis and Koutsika-Sotiriou^[19], found that crossing between recombinant lines may produce high yielding second-cycle hybrids. In such cases, General Combining Ability (GCA) is of small importance, since heterosis was found low and heterobeltiosis even lower (Table 2). When recombinant lines were crossed to unrelated free-release inbred lines, heterosis was found to be satisfactory and yielding performance was significant (Table 2). Similar data were reported by Vafias and Ipsilandis^[34], for recombinant lines in single and three-way crosses (Table 3). Tokatlidis^[45], tried to specify the optimum plant density for best field productivity of recycled maize hybrids and concluded that further improvement of hybrids is feasible by selection based on line single-plant selection in the absence of competition.

Table 3: Relative yield as percentage of F1 hybrid Costanza (%Costanza), Middle-parent Heterosis (MPH%), Heterobeltiosis to second parent in cross (SPHB%) and Heterobeltiosis to best parent (BPHB%) for best second-cycle crosses^[34]

Cross	%Costanza	MPH%	SPHB%	BPHB%
Marista X A3 RL	94	58	154	14
Costanza X A1 RL	92	16	58	-8
Prisma X A3 RL	90	49	143	8
RioGrande X A1 RL	81	5	38	-16
Costanza X A4 RL	80	24	169	-20
Prisma X A4 RL	80	41	168	-5
A4 RL X P6GR FR	90	171	201	147
A2 RL X Va26 FR	88	129	167	100
Costanza X B84 FR	98	47	195	-2
Prisma X Va26 FR	90	33	173	-12
Costanza X A1 RL	97	23	66	-3
Dracma X A1 RL	95	25	62	2
Prisma X A1 RL	88	10	52	-13
Costanza X A4 RL	87	33	190	-13
Dracma X A3 RL	83	28	123	-11
LG2360 X A1 RL	80	30	37	24
A3 RL X B84 FR	98	178	195	163
A4 RL X P6GR FR	95	185	216	159
A1 RL X Va26 FR	87	92	166	50
Costanza X B84 FR	104	56	214	4
Aligreen X Va26 FR	102	48	212	-3
Aligreen X B84 FR	101	46	206	-4
Costanza X P6GR FR	96	41	164	-4
Costanza X Va26 FR	91	37	177	-9
Rio Grande X A1 RL	100	32	71	8
Costanza X A1 RL	97	23	67	-3
Aligreen X A1 RL	96	18	65	-9
Rio Grande X A2 RL	92	34	110	-1
CS1251 X A4 RL	89	40	199	-9
Costanza X A4 RL	83	28	178	-17
Aligreen X A2 RL	80	7	82	-24
A1 RL X Va26 FR	98	116	200	69
A2 RL X Va26 FR	98	156	198	124
A1 RL X B84 FR	96	110	190	65
A4 RL X P6GR FR	84	153	181	130
Volusia X A1 RL	96	26	64	3
Costanza X A1 RL	88	11	51	-12
Costanza X A5 RL	86	33	194	-14
Costanza X A2 RL	86	19	96	-14
Prisma X A2 RL	81		86	
A1 RL X P6GR FR	87	84	140	50
A4 RL X Va26 FR	87	177	191	165
A5 RL X A1 RL	80	81	171	35
Costanza X A1 RL	99	25	70	-1
A4 RL X A2 RL	97	163	224	121
A3 RL X Va26 FR	87	147	164	133

Stability of performance: Total yield of crops is depended on three main factors, i.e., genes that control yield potential per plant, genes that confer tolerance to biotic and abiotic stresses and genes that control responsiveness to inputs^[15]. The Coefficient of Variation (CV)^[31,34,46] and other criteria^[15,16,38,46,47], were used to estimate stability of performance. Vafias and Ipsilandis^[34], used the CV as a criterion of stability for evaluation of three-way hybrids. These researchers found a few three-way crosses with low CV values, indicating stability of performance (Table 4). When selection for potential yield per plant was utilised for reconstructing cross

Table 4: The Coefficient of Variation % as a parameter of stability for years: 1998 (CV98), 1999 (CV99), 2000 (CV00), 2001 (CV01) and average CV (CVavg), only for crosses with average CV<10%³⁴

Crosses	CV98	CV99	CV00	CV01	CVavg
Costanza X Va26 FR	1	4	4		3
Marista X Va26 FR	3				3
Costanza X A1 RL	5.5	5	7	7	6.1
Lorena	6				6
Costanza X A4 RL	6.5	9	9		8.2
Rio Gande	6.5	9	9	7	7.9
Prisma X A1 RL	7.5	8			7.8
A1 RL X Va26 FR	8	9	9		8.7
A3 RL X B84 FR	8.5	9			8.8
Dracma	9	8			8.5
Costanza	10	8	10	8	9
Aligreen		9	10	9	9.3
A2 RL × Va26 FR	9		10		9.5
Prisma	11	9	11	9	10

B73XMo17 by developing new elite inbred parents, the stability (based on CV) of parents and the final hybrid was optimised^[46]. The dependence on high plant populations was related to stability of performance, when Tokatlidis *et al.*^[47] found that low CV is correlated to low plant population and high CV values to high plant population. Fasoulas^[33] reported the Prediction Criterion (PC), for evaluating high and stable performance. Lines derived directly from the F2 generation were superior to lines derived following previous population improvement, when ranked on the basis of PC. Fasoula and Fasoula^[17] analysed the components of crop yield for ensuring of high and stable performance and finally, they reported a complex criterion including yield potential per plant, tolerance to biotic and abiotic stresses and responsiveness to inputs, by estimating the standardized mean and the standardized selection differential in absence of competition for maximum yield performance per plant.

Criteria for recycling hybrids: The development of second-cycle (recycled) hybrids, is a common practice in maize breeding, since the F2 generations are considered a promising material for a breeding programme^[17,19,28,34,48].

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 (Fig. 5)^[49]. Low inbreeding depression, positive general combining ability and negative specific combining ability were found to be criteria for best promising starting material^[49]. Sotiriou *et al.*^[37] concluded that, in such cases the genetic background consists mainly of additive or partially dominant alleles. Ipsilandis^[28], Ipsilandis and Koutsika-Sotiriou^[19], reported that low inbreeding

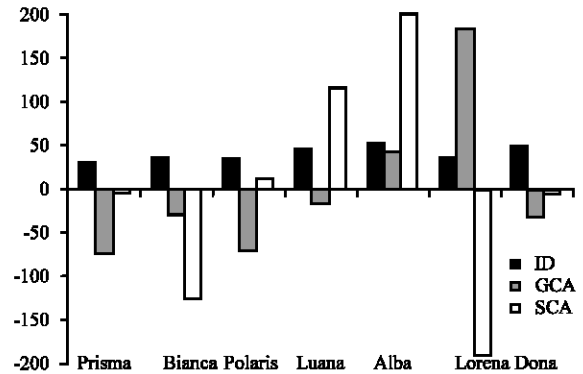


Fig. 5: Inbreeding depression (ID), General Combining Ability (GCA) and Specific Combining Ability (SCA) estimation for seven commercial F1 single maize hybrids, as criteria for hybrid reconstruction^[49]

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).

DISCUSSION

The indications that Half-sib families derived from F1 hybrid could outyield the original hybrid and additionally, a number of S1 families that out yielded the respective HS families, led Ipsilandis^[28] and Ipsilandis and Koutsika-Sotiriou^[19] to depict the important role of additive gene action. The presence of deleterious genes, reflected on yield distribution, as well as competition conditions and genetic mixing through hybridization, are considered masking conditions for phenotype evaluation^[23,38]. Negative correlation between yielding and competitive ability, nullifies heritability and leads to increasing CV values by increasing σ_p ^[23,38]. The larger the phenotypic standard deviation in a specific environment, as expressed by the magnitude of CV, the higher the load of defective genes and therefore the more reduced the buffering and tolerance to density^[38,47].

Data revealed that inbred lines are capable to reach hybrid performance. As far as the yielding capacity of inbred parents improves, the less the yield in F1 is favored by heterozygosity^[19,23]. In a few S1 families (in comparison to the HS), the favourable additive gene action was of greater importance than the heterozygote advantage of the corresponding HS families^[19]. Additive effects are heritable and as depicted here, are of greater importance in comparison to non-additive effects^[19,28,37]. Therefore,

the choice of hybrids instead of inbred lines as the end-products must rest on other non-genetic considerations. Dominance and pseudo-overdominance are coupled with genetic defects^[38]. This means that selection schemes aiming at exploiting dominant and pseudo-overdominant gene action lead to the preservation of defective genetic material. The presence of such defective genes reduces inbred line productivity and stability and also the ability of inbred parents to anticipate hybrid performance. Heterosis is beneficial when covers the genetic defects between alleles. Inbreds may be high yielding when are derived under pedigree line selection schemes evaluating *per se* performance under favourable conditions. Other products, such as three-way crosses with lower level of heterozygosity, may be more efficient and stable than single hybrids and more readily developed. These products depend their productivity on additive gene action^[19,34]. The impact on seed production is obvious: easier seed production because of higher productivity of basic materials and of course lower cost for seed companies. Fasoula and Fasoula^[15,16] reported a complex criterion for more reliable estimation of genetic materials. The use of this complex criterion in pedigree line selection schemes may lead to inbred line establishment as the final products of maize breeding programmes.

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