

The combining ability of recombinant S-lines developed from an F₂ maize population

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SUMMARY

Starting with the F₂ generation of the single-cross commercial hybrid Lorena (PR3183), recombinant lines were developed combining half-sib/S1 evaluation on widely spaced plants in the direction of high yielding *per se*. Combining ability tests consisted of crosses between: (a) recombinant lines of common pedigree and (b) recombinant lines and freely available inbred lines. The highest-yielding crosses between recombinant lines reached 100% of the original F₁ hybrid in a percentage of 14.2. Low heterosis was estimated owing to additive gene action of recombinant lines. Crosses between recombinant lines and freely available inbred lines outyielded significantly the commercial F₁ hybrid in a percentage of 33.3. Heterosis was greater and the original F₁ hybrid was outyielded significantly because of non-additive gene action. When the applied breeding procedure on a source population with high yield adaptability is adopted and where effects of intergenotypic competition masking the inherent genotypic value are controlled, population improvement may be substituted by combined half-sib/S1 selection for productivity of lines *per se* in low stress conditions during the very early stages.

INTRODUCTION

The plant breeder's choice of source germplasm determines the potential improvement for traits under selection in the breeding programme (Fountain & Hallauer 1996). Source germplasm used by maize breeders for inbred development includes primarily F₂ (elite × elite inbred crosses), backcross and synthetic populations (Bauman 1981). Jenkins (1978) 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.

Current maize breeders prefer genetically narrow-based populations (Hallauer 1979; Bauman 1981) including elite-line synthetics with a restricted genetic base, F₂ populations of single crosses and backcross populations. For a successful programme of recycling, the choice of the germplasm is the first priority (Duvick 1996). A successful breeding programme in developing new hybrids, depends not only on the germplasm but also on the procedure for developing inbred lines.

Considering maize, the final stage of a breeding

programme leads to the adaptation of heterosis. This dramatic phenomenon of increasing yields, is rendered on the function of alleles showing dominance effects (Smith 1984; Falconer 1989). According to Kearsley and Pooni (1992), heterosis is caused by dispersed genes showing directional dominance and not by heterozygote superiority or complementary epistasis.

The purpose of this study, was to explore combining ability effects in recombinant S-lines during a programme required to: (i) select for yield potential on a single-plant base, and (ii) start selection from the F₂ generation of a commercial single-cross maize hybrid. Pedigree selection or recurrent selection, contribute to genetic improvement of maize lines by increasing the frequency of favourable alleles and maintaining genetic variability for further selection (Lamkey & Hallauer 1984). The applied breeding programme aimed to rapidly develop inbred lines without the interference of selection cycles and recombination, based on: (i) a source population with high adaptability, (ii) controlling effects of intergenotypic competition, which during early stages mask the inherent genotypic value, (iii) maximizing differences in phenotypic values, and (iv) substituting population improvement by combined half-sib/S1 (HS-S1) selection for productivity of lines *per se* in low-stress conditions during the very early stages (Ipsilandis & Koutsika-Sotiriou 1997).

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MATERIALS AND METHODS

The source material, the F_2 generation of the single-cross commercial maize hybrid Lorena (PR3183) was chosen for this study. Lorena is well adapted and one of the highest yielding commercial maize single-cross hybrids in Greece. It was introduced into cultivation in the early 1980s and was withdrawn by the company Pioneer HiBred Int. in 1992. The hybrid possesses an optimum combination of favourable alleles for this region, as well as sufficient additive genetic variation in its F_2 generation (Hallauer & Miranda 1988) to guarantee a gain from selection.

Selection procedure

In 1987, selfed seed of the single-cross hybrid Lorena was produced by open pollination in an isolated field. The seed obtained was planted in 1988 as starting material and is indicated as generation S0 or F_2 . 1200 plants were utilized. The intra-row distance was 1.25 m and the inter-row distance was 1.08 m. Each hill was initially planted with a number of seeds and later thinned to one seedling to give a density of 0.8 plants/m². 512 S0 plants from the F_2 population were selected by eye on the basis of their vigour and prolificacy. The upper ear of each plant was selfed to produce S1 families and the lower ear was open-pollinated to produce the half-sib (HS) families. The HS families were used to describe the combining ability in early generations and in comparison to S1, the level of inbreeding depression (Ipsilandis 1996).

In 1989 the S1 lines from the selfed ear and the half-sib (HS) families from the open-pollinated ear of each of 512 F_2 plants, were evaluated in comparison to the original single-cross hybrid PR3183. The evaluation was made by means of a moving block design (Fasoulas 1985). The entries in the field were located in such a way that every S1 row was adjacent to the corresponding HS family (512 pairs S1-HS). Hybrid PR 3183 was the check and was sown in 64 rows. The intra-row distance was 40 cm and the inter-row distance 1 m. The density was 2.75 plants/m². The plots consisted of 4 m long single rows of 11 plants. From each S1 line, a single plant was randomly selected and selfed. Fifty S1 lines (10%) were selected according to the relative difference in yield with regard to the corresponding HS-family.

Combining ability tests

Three kinds of crosses were performed: (a) formation of HS families, (b) diallel crosses between S4 and S5 recombinant lines, and (c) crosses of these lines with freely available inbred lines. In 1992, S4 recombinant lines were crossed as a diallel. In parallel, S4 lines were also crossed to B73, a well-known free-release inbred line. In 1993, S5 recombinant lines were crossed as a second diallel. In 1994 and 1995, S6 and S7 lines were

crossed to the freely available inbred lines: B84, Va22, Va26, 5C (Koutsika-Sotiriou *et al.* 1990) and P-6 (Efthimiadis & Tsiftaris 1996). These crosses were evaluated in 1993, 1994, 1995 and 1996 respectively. 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/m². The F_1 single-cross hybrid Lorena (PR3183) was used as the main check and another Pioneer Hibred Int. F_1 single-cross hybrid Dona (PR3165) as a second check. S5-lines were evaluated in a separate experiment. 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.

Data analyses

The RCB analysis was based on the null hypothesis by means of an analysis of variance at the 0.05 probability level (Gomez & Gomez 1984).

General combining ability for HS families was computed as the difference in yielding performance for each family in relation to the mean performance for HS (HS mean yield). Inbreeding depression was computed according to the formula (Goulas & Lonnquist 1976):

$$\left(1 - \frac{\text{S1 mean yield}}{\text{HS mean yield}}\right) \times 100.$$

The diallel analysis for General Combining Ability (GCA), was performed using the following formula (Falconer 1989): $GCA = (\bar{A} - \bar{X})(n-1)/(n-2)$.

Heterosis (%) was computed by the formula: $H = (F_1 - MP)/MP \times 100$, where F_1 = the hybrid yield, MP = the middle parent yield.

Heterobeltiosis (%) was computed by the formula: $HB = (F_1 - P)/P \times 100$, where F_1 = the hybrid yield and P = the best parent yield or the second parent yield (Koutsika-Sotiriou & Bos 1996).

RESULTS AND DISCUSSION

General combining ability of half-sib families

The general combining ability (GCA) of HS families showed a normal distribution (Fig. 1). The percentage of deleterious genes (equivalent to inbreeding depression percentage) was estimated to be 40%, according to Fasoulas (1988, 1993). The inbreeding depression distribution (Fig. 2) showed that the most common values were about 25–30%, as many S1 families were inferior to the corresponding HS families with the same percentage. The mean percentage (40%) in this study was lower than the 70% found by Horner *et al.* (1969) followed by population im-

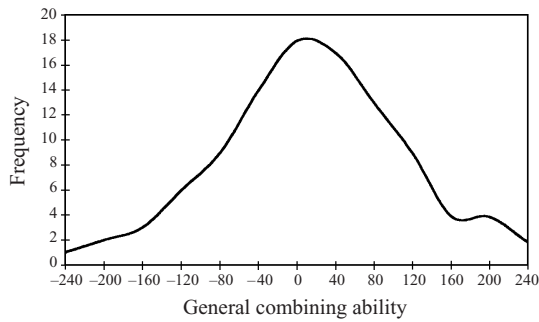


Fig. 1. The general combining ability (GCA) frequency distribution of HS families.

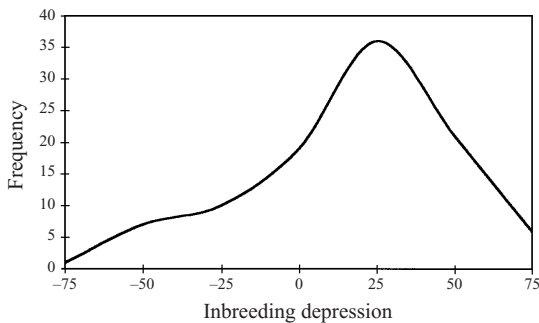


Fig. 2. The inbreeding depression frequency distribution of S1 families.

provement using S2 families, thus being promising for better improvement in the present breeding programme.

The combining ability for some HS families was high and their yielding performance was greater than the original F_1 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 F_1 single-cross hybrid (Genter & Alexander 1966; Genter 1973; Fasoulas 1993). 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.

Crosses between recombinant lines

Single-cross hybrids between S4 or S5 lines, such as D-17 \times C-22, D-17 \times A-27 and D-17 \times C-33 reached 100% of the original single-cross hybrid yield (Table 1). It is possible for these lines to belong to the same heterotic group and this would eliminate the chances for heterotic gene action. This could be an additional

problem for realizing heterosis after practicing diallel crosses between lines of common pedigree.

The performance of the recombinant lines in their crosses, was in relation to the performance *per se* of these lines, and thus the better yielding recombinant lines gave the best hybrids (Tables 1 and 3). The performance of common-pedigree recombinant lines depends mainly on additive effects, in the way that the best yielding line D-17 gave the best second-cycle hybrids. Genter & 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*. It is possible, that selection practiced for improving line performance *per se*, lead to the accumulation of favourable additive genes. These results are in accordance to Sotiriou *et al.* (1996), who concluded that, in such cases the genetic background consists mainly of additive or partially dominant alleles.

General combining ability (GCA) is of small importance, since heterosis was low (60% at the most, Table 1) and heterobeltiosis was even lower (43% for best parent, Table 1). These crosses derived their yielding performance from favourable additive gene effects, common in the two parents (Table 3) and consequently the second-cycle hybrids between them must be in a lower level of heterozygosity compared to the original hybrid (Genter 1967; Koutsika-Sotiriou *et al.* 1990; Fasoulas 1993). Heterosis was not expected to be great owing to the common-pedigree or relatedness of recombinant lines. In such cases, the additive effects would be significant because the favourable genes present in the two parents were exactly the same in a large proportion, as the recombinant lines would be closely related after selection practiced from the F_2 generation to S6 to improve performance *per se*. Additionally, the possibility that these lines belonged to the same heterotic group would not allow heterosis to be expressed. Crosses within the same heterotic group probably were in coupling-phase linkages since no dramatic heterosis was found (Sughrue & Hallauer 1997). Maybe the final target is improvement of yield potential *per se* and not heterosis, since this improvement proved to be feasible in the absence of satisfactory heterosis. Genter (1973) stated that the combining ability must lead to improved performance and not higher heterosis.

Heterosis (Fasoula & Fasoula 1997) regardless of the theory involved (dominance or over-dominance), prevails in the presence of non-additive alleles (pseudo-overdominant alleles) and thus the production of F_1 hybrids is accompanied by two serious disadvantages: (1) it contributes to the accumulation and preservation of deleterious genes and (2) it does not exploit additive alleles which are solely responsible for genetic advance through selection and release of transgressive segregation (Koutsika-Sotiriou *et al.*

Table 1. *Relative yield (%) to Lorena, middle-parent heterosis (%), heterobeltiosis to best parent and to second parent (%) for crosses between S4 and S5 recombinant lines*

Crosses	Yield (%) Lorena	Middle-parent heterosis (%)	Heterobeltiosis to best parent	Heterobeltiosis to 2nd parent
Crosses between S4 recombinant lines				
LORENA*	100	—	—	—
D-17 × C-22	100	+60	+43	+82
D-17 × C-33	88	+36	+26	+46
D-17 × C-35	81	+20	+15	+25
D-17 × A-27	80	+37	+14	+60
A-27 × B-29	80	—	+43	—
A-27 × C-10	77	+47	+40	+54
A-27 × C-33	72	+26	+31	+20
A-27 × C-35	70	+18	+27	+8
D-17 × D-1	65	+12	−7	+30
A-27 × A-8	50	−16	−9	−23
A-27 × C-22	47	−15	−15	−15
Crosses between S5 recombinant lines				
LORENA†	100	—	—	—
D-17 × A-27	100	+60	+43	+82
D-17 × C-22	100	+60	+43	+82
D-17 × C-33	99	+52	+41	+65
D-17 × A-8	89	+32	+27	+37
D-17 × D-27	89	+78	+27	+197
D-17 × C-27	83	+66	+19	+177
D-17 × B-24	82	+52	+17	+87
D-17 × D-5	80	—	+14	—
D-17 × D-30	77	+40	+10	+92
A-27 × A-8	70	+17	+7	+27

* Lorena 100 = 14300 ± 840 kg/ha ($CV_{exp} = 16\%$).

† Lorena 100 = 14200 ± 720 kg/ha ($CV_{exp} = 15\%$).

1990; Xiao *et al.* 1995). Transgressive segregation enhances response through selection and establishes the superiority of the inbred over hybrid vigour and also of the semidominant over codominant or overdominant alleles (Fasoula & Fasoula 1997).

The correlations in Table 4 showed that r coefficient was very low for the two variables heterobeltiosis to best parent and heterobeltiosis to second parent, due to the differences in the behaviour of the two parents. These differences were selected on purpose, when S1 and HS families were evaluated and different yielding performance was found. These differences were expressed in the inbreeding depression percentage (Table 3). The yield showed a very strong and positive correlation with middle-parent heterosis and heterobeltiosis to best parent, but not with heterobeltiosis to second parent. The best parent yield may contribute significantly in the yield of its crosses (Genter 1967) and heterobeltiosis to this parent is closely related to the yield of their hybrids. This is due only to heritable gene action, i.e. the additive proportion of gene action. This is clearly shown in the S5 generation, where the correlation between the yield of the crosses and the heterobeltiosis to best parent was significant at $P < 0.01$ with an $r = 0.99$. In the S4 generation all

the correlations were significant too. The expected middle-parent heterosis (MP) when crossing recombinant lines would be computed by the following equation: $MP = -79.46 + 1.443Y$, where Y is the yield of the hybrid, and the heterobeltiosis to best parent (BP) by the equation: $BP = -59.23 + 1.004Y$. In general, the prediction of what a breeder can expect trying to profitably utilize combining ability, is not so difficult when recombinant lines are involved (Torregroza & Harpstead 1965; Toledo *et al.* 1984).

Crosses between recombinant lines and freely available inbred lines

When S6 and S7 recombinant lines were crossed to freely available inbred lines with different pedigrees (Smith 1988; Smith *et al.* 1992), heterosis was much greater (up to 175%) and heterobeltiosis doubled the performance of the best parent (Table 2). Six crosses outyielded Lorena, by 10% or more and these differences were significant at least in one year of comparisons, at the 5% level. In these crosses, the middle-yielding lines C-22, A-27 and C-33 gave heterotic single-cross hybrids, in contrast to D-17 which gave only one heterotic cross (10% over Lorena

Table 2. *Relative yield (%) to Lorena, middle-parent heterosis (%), heterobeltiosis to best parent and to second parent (%) for crosses between recombinant lines and freely available inbred lines*

Crosses	Yield (%) Lorena	Middle-parent heterosis (%)	Heterobeltiosis to best parent	Heterobeltiosis to 2nd parent
Crosses between unrelated lines				
DONA	118	—	—	—
C-22 × Va26	117	+175	+113	+290
C-22 × 5C	113	+105	+105	+105
C-22 × B84	112	+164	+104	+273
A-27 × Va26	112	+164	+104	+273
C-33 × P-6	111	+122	+85	+177
D-17 × Va26	110	+120	+57	+267
C-22 × P-6	109	+129	+98	+172
C-22 × Va22	106	+165	+93	+324
A-27 × 5C	105	+91	+91	+91
D-17 × 5C	100	+60	+43	+82
LORENA*	100	—	—	—
C-33 × Va22	98	+131	+63	+292
D-17 × B84	98	+96	+40	+227
D-17 × Va22	92	+94	+31	+268
D-17 × P-6	92	+67	+31	+130
C-22 × B73	69	+72	+25	+176
A-27 × B73	59	+47	+7	+136
A-8 × B73	44	—2	—32	+76
D-17 × B73	40	—16	—43	+60

* Lorena 100 = 15600 ± 1420 kg/ha (CV_{exp} = 16%).Table 3. *Relative yield (%) to Lorena and to inbred line B73, inbreeding depression and mean general combining ability (GCA) for lines involved in crosses*

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.

Table 4. Summarized correlations between the variables of Tables 1 and 2

Variables	MP	BP	SP
Unrelated lines (recombinant lines \times freely available inbred lines)			
Yield % Lorena (Y)	0.88**	0.93**	0.55*
Middle-parent heterosis % (MP)	—	0.92**	0.82**
Heterobeltiosis to best parent (BP)	—	—	0.52*
Heterobeltiosis to 2nd parent (SP)	—	—	—
S4 & S5 recombinant lines			
Yield % Lorena (Y)	0.86**	0.86**	0.59*
Middle-parent heterosis % (MP)	—	0.76*	0.88**
Heterobeltiosis to best parent (BP)	—	—	0.40
Heterobeltiosis to 2nd parent (SP)	—	—	—
S4 recombinant lines			
Yield % Lorena (Y)	0.93**	0.82*	0.91**
Middle-parent heterosis % (MP)	—	0.89**	0.96**
Heterobeltiosis to best parent (BP)	—	—	0.72*
Heterobeltiosis to 2nd parent (SP)	—	—	—
S5 recombinant lines			
Yield % Lorena (Y)	0.56	0.99**	0.06
Middle-parent heterosis % (MP)	—	0.50	0.84*
Heterobeltiosis to best parent (BP)	—	—	0
Heterobeltiosis to 2nd parent (SP)	—	—	—

Marked correlations are significant (*) at $P < 0.05$ level (**) at $P < 0.01$ level.

when crossed to Va26, Table 2). The C-22 recombinant line, showed about 5% better performance in its crosses compared to D-17 and heterosis was 50% greater. Five C-22 crosses had better or equal yields to the only cross of D-17 that outyielded the original hybrid Lorena. When these lines were crossed to lower yielding freely available inbred lines, some of the favourable additive effects were lost. This loss of favourable additive gene action could not be replaced by heterotic effects of a satisfactory level, because of lack of such loci in the high yielding inbred lines. The possibility for heterotic effects was very low, as the performance of high yielding recombinant lines was based mainly on additive genes which represent the greatest proportion of gene action, although the differences in heterotic groups would be possibly large (Smith *et al.* 1992). Inbreds from the opposite heterotic group are more likely to have different alleles influencing yield. Crosses between such selected lines possibly were in repulsion-phase linkages (Sughrue & Hallauer 1997).

Correlations between the yield, middle-parent heterosis, heterobeltiosis to best parent and heterobeltiosis to second parent, were significant (Table 4). The yield of the crosses between the recombinant lines and freely available inbred lines was strongly related to middle-parent heterosis and heterobeltiosis to best parent, as it was found for correlations between recombinant lines. The behaviour of these unrelated lines was similar to the behaviour of the recombinant lines, and the expected middle-parent heterosis (MP) would be computed by the equation:

$MP = -88.02 + 1.997Y$, where Y is the yield of the hybrid, and the heterobeltiosis to best parent (BP) by the equation: $BP = -115.3 + 1.832Y$. In comparison with the equations for recombinant lines, middle-parent heterosis can be more easily realized when unrelated lines are crossed. From the equations, the yield of the crosses must be at least 45% of the tester yield considering unrelated lines and 56% considering recombinant lines to realize middle-parent heterosis. The correlation between yield and the heterobeltiosis to best parent was very significant and the r coefficient reached 0.93. The additive proportion of gene action was very important, as was found for correlations between recombinant lines.

S5 line performance, per se

It is well known that breeding of a maize source population is considered to be an effective way to enhance the development of superior inbred lines (Sprague & Eberhart 1977) and that proper choice of germplasm determines the ultimate success of selection for genetic improvement (Fountain & Hallauer 1996). The present high yield adaptability procedure started with S1 families with a mean yield corresponding to 32% of the original hybrid (Lorena) and improved to 46% for S5 or 42% for S6 of this percentage (Ipsilandis & Koutsika-Sotiriou 1997). The best S5 recombinant lines yielded from 50% to 70% of the yield of the original single-cross hybrid (Lorena), while the B73 inbred line yielded only 25% (Table 3). The recombinant line D-17 was the highest

yielding line *per se* (70% of Lorena) due to the accumulation of favourable additive genes (Fasoulas 1988; Ipsilandis & Koutsika-Sotiriou 1997). Also from diallel crosses trials (Table 3), 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. The inbred lines Va26 and B84 showed the best contribution in general combining ability in crosses (Table 3). The high yielding capacity of recombinant lines is owed to the fact that deleterious genes were replaced by favourable alleles. As far as the yielding capacity of inbred lines improves, the less the yield in F_1 is favoured by heterozygosity (Koutsika-Sotiriou *et al.* 1990; Fasoulas 1993).

In conclusion, the data showed that production of vigorous inbred lines approaching hybrid productivity was achieved when selection for combining ability was replaced by selection for inbred line performance *per se*, so deleterious genes could be effectively removed. Efficient selection for line performance *per se* applied from the F_2 generation of the single-cross hybrid Lorena was accompanied by the development of an inbred line with 70% of the productivity of hybrid Lorena. This is remarkably above the 50% of hybrid potential for current elite inbreds and provides evidence that inbred lines may reach the yield potential and stability of hybrids once efficient breeding methodology is used.

REFERENCES

- BAUMAN, L. F. (1981). Review of methods used by breeders to develop superior corn inbreds. *Proceedings Annual Corn and Sorghum Industrial Research Conference* **36**, 199–208.
- DUVICK, D. N. (1996). Plant breeding, an evolutionary concept. *Crop Science* **36**, 539–548.
- EFTHIMIADIS, P. & TSAFTARIS, A. (1996). The use of biochemical markers for distinguishing maize inbred lines. In *Proceedings 6th Hellenic Conference. The Greek Scientific Society for Plant Breeding*, Florina, 2–4 October 1996, pp. 396–403.
- FALCONER, D. S. (1989). *Introduction to Quantitative Genetics*, 3rd edn. London: Longman.
- FASOULA, D. A. & FASOULA, V. A. (1997). Gene action and plant breeding. *Plant Breeding Reviews* **15**, 315–374.
- FASOULAS, A. C. (1985). A moving block evaluation technique for improving the efficiency of pedigree selection. *Euphytica* **36**, 473–478.
- FASOULAS, A. C. (1988). *The Honeycomb Methodology of Plant breeding*. Thessaloniki: A. Altidjis.
- FASOULAS, A. C. (1993). *Principles of Crop Breeding*. Thessaloniki: A.C. Fasoulas.
- FOUNTAIN, M. O. & HALLAUER, A. R. (1996). Genetic variation within maize breeding populations. *Crop Science* **36**, 26–32.
- GENTER, C. F. (1967). Inbreeding without inbreeding depression. In *Proceedings, 22nd Hybrid Corn Industry—Research Conference*, pp. 82–90. Washington DC: American Seed Trade Association.
- GENTER, C. F. (1973). Comparison of S1 and testcross evaluation after two cycles of recurrent selection in maize. *Crop Science* **13**, 524–527.
- GENTER, C. F. & ALEXANDER, M. W. (1966). Development and selection of productive S1 inbred lines of corn (*Zea mays* L.). *Crop Science* **6**, 429–431.
- GOMEZ, K. A. & GOMEZ, A. A. (1984). *Statistical Procedures for Agricultural Research*, 2nd edn, pp. 20–30. Singapore: John Wiley & Sons.
- GOULAS, C. K. & LONNQUIST, J. H. (1976). Combined half-sib and S1 family selection in a maize composite population. *Crop Science* **16**, 461–464.
- HALLAUER, A. R. (1979). *Corn Breeding Opportunities in the 1980s*. Des Moines IA: Annual Corn Iowa Seed Dealers Association.
- HALLAUER, A. R. & MIRANDA FO, J. B. (1988). *Quantitative Genetics in Maize Breeding*, 2nd edn. Ames, IA: Iowa State University Press.
- HORNER, E. S., CHAPMAN, W. H., LUTRICK, M. C. & LUNDY, H. W. (1969). Comparison of selection based on yield of topcross progenies and of S2 progenies in maize (*Zea mays* L.). *Crop Science* **9**, 539–543.
- IPSIANDIS, K. (1996). *The possibility to predict combining ability between maize inbred lines based on best cross performance*. PhD Thesis, Department of Genetics and Plant Breeding, Aristotle University of Thessaloniki, Greece.
- IPSIANDIS, K. & KOUTSIKA-SOTIRIOU, M. (1997). High line performance *per se* under low stress conditions. In *XVIIIth Conference on Genetics, Biotechnology and Breeding of Maize and Sorghum* (Ed. A. Tsafaris), pp. 191–196. Thessaloniki: EUCARPIA.
- JENKINS, M. T. (1978). Maize breeding during the development and early years of hybrid maize. In *Breeding and Genetics. Proceedings International Maize Symposium* (Ed. D. B. Walden), pp. 396–403. New York: John Wiley & Sons.
- KEARSEY, M. J. & POONI, H. S. (1992). The potential of inbred lines in the presence of heterosis. In *Reproductive Biology and Plant Breeding* (Eds Y. Dattee, C. Dumas & A. Gallais), pp. 371–386. London: Springer-Verlag.
- KOUTSIKA-SOTIRIOU, M. & BOS, I. (1996). Heterosis after several numbers of cycles of mass honeycomb selection in maize. *Journal of Genetics and Plant Breeding* **50**, 7–14.
- KOUTSIKA-SOTIRIOU, M., BOS, I. & FASOULAS, A. (1990). Hybrid reconstruction in maize. *Euphytica* **45**, 257–266.
- LAMKEY, K. R. & HALLAUER, A. R. (1984). Comparison of maize populations improvement by recurrent selection. *Maydica* **19**, 357–374.
- SMITH, J. S. C. (1988). Diversity of United States hybrid maize germplasm; isozymic and chromatographic evidence. *Crop Science* **28**, 63–69.
- SMITH, O. S. (1984). Comparison of effects of reciprocal recurrent selection in the BSSS(R), BSCB1(R) and BS6 population. *Maydica* **24**, 1–8.
- SMITH, J. S. C., SMITH, O. S., WRIGHT, S., WALL, S. J. & WALTON, M. (1992). Diversity of U.S. hybrid maize germplasm as revealed by Restriction Fragment Length Polymorphisms. *Crop Science* **32**, 598–604.
- SOTIRIOU, A., KOUTSIKA-SOTIRIOU, M. & GOULI-VAV-

- DINOUDI, E. (1996). The effect of honeycomb selection for grain yield on a maize population. *Journal of Agricultural Science, Cambridge* **127**, 143–149.
- SPRAGUE, G. F. & EBERHART, S. A. (1977). Corn breeding. In *Corn and Corn Improvement, 2nd edn.* (Ed. G. F. Sprague), pp. 305–362. Madison WI: American Society of Agronomy.
- SUGHROUE, J. R. & HALLAUER, A. R. (1997). Analysis of the diallel mating system for maize inbred lines. *Crop Science* **37**, 400–405.
- TOLEDO, DE, J. F. F. POONI, H. S. & JINKS, J. L. (1984). Predicting the properties of second cycle hybrids produced by intercrossing random samples of recombinant inbred lines. *Heredity* **53**, 283–292.
- TORREGROZA, M. & HARPSTEAD, D. D. (1965). Performance of S1 lines of maize *per se* and as test crossed to related and unrelated varieties. *American Society of Agronomy. Agronomy Abstracts*. 21 pp.
- XIAO, J., LI, J., YUAN, I. & TANKSLEY, S. D. (1995). Dominance is the major genetic basis of heterosis in rice as revealed by QTL analysis using molecular markers. *Genetics* **140**, 745–754.