RESEARCH ARTICLE

Hybrid improvement and reconstruction based on prognostic breeding selection criteria

Constantinos G. Ipsilandis^{1*}, Vasileios Greveniotis², Panagiota Pampouktsi¹, Evangelia Sioki³, Fanis A. Tsapikounis⁴

¹Regional Administration of Central Macedonia, Department of Agriculture, Thessaloniki 54622, Greece, ²Department of Agricultural Technology, Technological Educational Institute of Thessaly, Larissa 41110, Greece, ³Department of Agricultural Economics, Aristotle University of Thessaloniki, Thessaloniki 54124, Greece, ⁴FytoDiagnosi, Plant Clinic, 36 Deligianni Str, Pirgos 27100, Greece

ABSTRACT

In order to faster and more efficiently select maize inbred lines as parents for maize hybrids, a multi-year evaluation was conducted under both honeycomb methodology schemes and classic randomized complete block designs. Combined yield and stability calculations were used. The initial genetic material was developed from F2 of a commercial F1 maize hybrid.1200 F2 plants were used at an intrarow distance of 1.25 m and the inter-row distance was 1.08 m in a NR-0 honeycomb design. Combined Half-sib and S1 evaluation was performed for oriented crosses. After successive selfing generations S1 to S7 progenies were developed. Three types of crosses were performed a) Formation of HS families, b) Diallel crosses between S4 and also S5 recombinant lines, and c) Crosses of these lines to the freely available inbred line B73. Crosses between high yielding S-lines to common foreign parent led to limited heterotic phenomena and relative low yielding performance. Heterobeltiosis was found near zero or negative, proving that such kind of parents cannot contribute in high yielding crosses because of the accumulation of useful additive alleles in the improved parent, and additive alleles are not favoured in heterozygote condition. Crosses between improved lines were generally high, but they based their productivity mainly on additive gene action. Prognostic breeding is more accurate when selection is applied for exploitation of additive gene action. CV was a good stability criterion, but CC proved confusing for selecting crosses. Productivity index *P* exhibited the superiority of the best lines that showed high and stable performance across years. The procedure resulted in high yielding inbred lines bypassing population improvement and thus shortened the whole evaluation process.

Keywords: Additive genes; Crosses; Productivity index P; Second-cycle

INTRODUCTION

Modern maize (Zea mays L.) breeders prefer genetically narrow-based populations (Hallauer, 1979) including eliteline synthetics of narrow genetic base, F2 populations of single crosses and backcross populations. Thus, inbred development includes primarily elite inbred crosses, backcross and synthetic populations (Bauman, 1981). For successful genetic recycling, the choice of elite germplasm is very important (Fasoulas, 1988; Duvick, 1996). Developing new hybrids depends not only on the germplasm but also on the selection procedure for developing inbred lines to serve as hybrid parents, which is the final target considering maize. Hybrid yield is depended mainly on heterosis which improves total field performance of maize plants and is attributed mainly on dominant allele effects (Smith,

1984; Falconer, 1989; Kearsey and Pooni, 1992). Fasoulas (1988, 1993) considered that heterosis, although a positive phenomenon (Fehr, 1987), has a "dark side" by encrypting deleterious recessive alleles in heterozygote loci found in repulsing phase linkage. Thus, "pseudo-overdominant" effects may occur in such cases and the positive dominant allele plays a double role: a positive addition on yield and deleterious recessive repression.

The yielding distance between F_1 maize hybrids and inbred lines or F_2 generations was found significant (Vafias and Ipsilandis, 2005) as a result of exploitation of heterosis (Tollenaar et al., 2004). Ipsilandis et al. (2006) reported that hybrid reconstruction by recycling may lead to the exploitation of positive additive gene action. This is a result of *per se* improvement of inbred lines based on

*Corresponding author:

Constantinos G. Ipsilandis, Regional Administration of Central Macedonia, Department of Agriculture, Thessaloniki 54622, Greece. **E-mail:** ipsigene@gmail.com

Received: 11 January 2019; Accepted: 24 May 2019

additive genes that increase yielding performance. This procedure may avoid population improvement since productivity is based on already improved lines (Ipsilandis & Koutsika-Sotiriou, 2000). As far as parental inbred lines yield improves, the less F1 cross yielding performance depends on heterosis and heterozygosity (Ipsilandis et al., 2005). Thus, it is important to have elite inbred lines with high productivity in order to partly support yield of modern maize hybrids and also to ensure sufficient (and cheap) seed production (Duvick, 1999, 2001; Ipsilandis & Koutsika-Sotiriou, 2000). Additionally, Crow (2000) also reported that additive genetic action (with partial to complete dominance) is the dominant kind of gene action in the expression of yield in maize. Nevertheless, Midparent heterosis (Fehr, 1987) expressed as yield superiority of the hybrid in comparison to its parents is still the final product of a breeding program, resulting in high yielding and stable genetic materials.

Prognostic breeding is a new approach to accelerate the progress of genetic improvement through selection by evaluating two main components: plant yield potential and stability of performance (Greveniotis and Fasoula, 2016). Plant yield and stability are calculated using plant prognostic equations. They reported that prognostic breeding led to the isolation of superior maize lines whose productivity was comparable to F1 commercial single-cross hybrid Costanza (around 90% of yielding performance). Across all cycles, the average annual genetic gain ranged from 23% to 36% by applying honeycomb methodology selection schemes. The novelty in prognostic honeycomb methodology is that evaluation for yield and stability genes is accomplished in the same generation by evaluating the crop yield potential of each individual plant. Many formulas were proposed previously to accelerate the breeding procedure under honeycomb methodology schemes. In historic basis, Fasoulas (1981) and Koutsika-Sotiriou (1985), proposed combination of mean yield and Coefficient of Variation (CV%) for estimating productivity and stability together with productivity index P, a statistical parameter (%) measuring statistically differences (estimated distances) between the mean values of genetic materials and thus showing how many progeny families of a genetic material are statistically superior. This was the first attempt to improve and shorten the whole evaluation procedure.

Then, the combined criterion CC was initiated for selecting superior genotypes (Fasoula-Ioannides, 1992): $CC = \bar{x}^2 (\bar{x} - s)/s$ where \bar{x} and s are the progeny line mean and standard deviation. Koutsika-Sotiriou and Bos (1996) proposed another criterion for evaluating maize inbred lines to be used as hybrid parents: Heterobeltiosis (%) as computed by the formula: HB = (F1-P)/P x 100, where

F1 = the hybrid yield and P = the best parent yield or the second parent yield.

Later the A and B prediction and selection formulas were proposed (Fasoula, 2008):

 $A = (x/\bar{x}_r)^2 \cdot (\bar{x}/s)^2$ and $B = (\bar{x}/\bar{x}_t)^2 \cdot (\bar{x}/s)^2$ where x is the single-plant yield, \bar{x}_r is the average yield of the surrounding plants within a moving ring of a chosen size, \bar{x}_t is the overall experimental mean and \bar{x} and s are the progeny line mean and standard deviation. Now the new formula pPE is used (Greveniotis and Fasoula, 2016): pPE = $(x/\bar{x}_r)^2 \cdot (\bar{x}_g/s)^2$ where x is the single-plant yield, \bar{x}_r is the average yield of the surrounding plants within a moving ring of a chosen size, \bar{x}_g is the mean plant yield of each moving grid and s is the standard deviation.

In order to faster and more efficiently select maize inbred lines as parents for maize hybrids, a multi-year, multi-criteria evaluation was conducted under both honeycomb methodology and classic randomized complete block schemes. Combined plant yield and stability estimations were used and the progress of inbred lines per se and their crosses were recorded across generations. The procedure also estimated the efficiency of the criteria used during genotype evaluation.

MATERIALS AND METHODS

The initial genetic material was developed from F2 generation of a commercial F1 single-cross maize hybrid (Lorena, PR3183), one of the most adapted commercial hybrids in Greece. All field experiment was established at the University Farm of Thessaloniki in northern Greece (22°59° E, 40°32° N). Local conditions are recorded for a 10-year period (1988-1997) in the archives of the National Meteorogical Society (Greece).

1200 F2 plants were used at an intra-row distance of 1.25 m and the inter-row distance was 1.08 m in a NR-0 honeycomb design (Fasoulas, 1981). Each hill was initially planted with a number of seeds and later it was thinned to one seedling to form an ultra-low density of 0.8 plants·m⁻². A total of 512 S0 plants from the F2 population were chosen by eye-selection 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.

Next year (first year of evaluation), the S1 lines from the selfed ear and the half-sib (HS) families from the open-pollinated ear of each of 512 F2 plants, were evaluated in comparison to the original single-cross hybrid PR3183. The

evaluation was made in single progeny line under a moving block design (Fasoulas, 1985; Ipsilandis, 1996). 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 control and sown in 64 rows. The intra-row distance was 40 cm and the inter-row distance 1 m. The density was 2.75 plants m⁻². The plots consisted of 4 m long single rows of eleven plants. From each S1 line, a single plant was randomly selected and selfed. Fifty S1 lines (about 10%) were selected to form S2 seed, according to the relative difference in yield with regard to the corresponding HS-family. The HS families were used as initial testers for combining ability in early generations. After successive selfing generations S4, S5, S6 and S7 progenies were developed. Coding of lines was based on line classification according to their S1/HS performance.

Across years, three types of crosses were performed: a) Formation of HS families, b) Diallel crosses between S4 and also S5 recombinant lines, and c) Crosses of the most promising of these lines to freely available inbred line B73 as common parent (Ipsilandis, 1996). Crosses were categorized and programmed after grouping parental inbred lines in yield categories according to their S1 per se yield and HS yield (Goulas & Lonnquist, 1976; Coors, 1988; Ipsilandis, 1996). Line classification and S1/ HS yield level are presented in Table 1 (two groups 1 and 4 were split in two subgroups). These crosses across years and generations were evaluated in Randomized Complete Block (RCB) designs 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 consisted of 50 plants, i.e. 25 plants per row giving a population density of 6.25 plants m⁻². The initial F1 single-cross hybrid was included as the main control (PR3165 was also included). The S5, S6 and S7 inbred progenies were evaluated in a separate experiment. Additionally, honeycomb evaluation was used for S3 progenies and their S2 crosses in replicated honeycomb designs (R-133) at the ultra-low density of 0.8 plants m⁻² (Fasoulas, 1988; Ipsilandis, 1996; Ipsilandis et al., 2006; Greveniotis & Fasoula, 2016). All plants were grown using conventional fertilizer applications and weed/ pest control in order to promote high productivity. Grain yields were adjusted 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 & Gomez, 1984). Proper data handling and moisture adjustment were performed and statistical analysis was made by MSTAT-C academic statistical package. Combined criterion was applied according to Fasoula-Ioannides (1992). Productivity ratio P, was calculated according to Koutsika-Sotiriou (1985). Equation B for honeycomb family selection was applied properly according to Fasoula (2008). Coefficient of variation (CV) and data rendering were processed according to Ipsilandis (1996) and, Ipsilandis & Koutsika-Sotiriou (2000), and CV values were used in the sense of stability estimation as described by Greveniotis et al. (2018, 2019).

RESULTS

Table 1 presents the s-line classes and their S1/HS productivity (in g/plant) and stability according to CV values. Great differences in means were found between classes including, combinations of high yielding S1 or HS progenies and their middle to low-yielding HS or S1 respective progenies. In some cases, S1 and HS progenies exhibited high productivity simultaneously. S2XS2 crosses productivity was evaluated in honeycomb design and great differences were revealed (Table 2). Some crosses like A-27XD-17 showed high productivity and the F1

Table 1: Classification of S1 families, their per se yield mean (in g/plot), Half-sib (HS) mean, standard deviations (Std Dev.) and coefficient of variation (CV%)

No	Class	Progeny	Families	Mean	Std. Dev.	CV%
1	1	S1	48	2648	696	26
		HS		2130	776	36
2	1A	S1	8	2890	114	4
		HS		2570	266	1
3	2	S1	20	1500	420	28
		HS		5390	610	11
4	3	S1	16	2880	349	12
		HS		4640	506	11
5	4	S1	24	3275	246	7.5
		HS		3790	342	9
6	4A	S1	16	3000	210	7
		HS		3840	510	13
7	5	S1	16	2661	298	11
		HS		4000	380	9.5
8	6	S1	6	1975	107	5.5
		HS		1650	400	24

Table 2: S2XS2 crosses between inbred lines and their mean yield (in g/plant) in honeycomb R-133

No	Cross	Mean
1	A-27 X D-17	1930
2	A-27 X G-22	1455
3	A-8 X D-5	1315
4	G-35 X D-11	920
5	B-26 X G-27	785
6	B-24 X D-17	775
7	D-27 X G-10	765
8	B-36 X D-1	700
9	A-1 X D-2	630
10	B-14 X A-29	600
11	A-10 X B-29	585
12	G-10 X A-22	570
13	G-20 X D-8	570
14	PR3183	517

control exhibited low yields of individual plants. S5 line productivity is presented in Table 3. The use of productivity index *P* value showed that high yielding lines like D-17 and A-8 exhibited also high *P*-values. Also A-27 seemed to be a promising line according to *P* values, although not so productive according to recorded yield (7800 Kg per Ha) in comparison to D-17 (13000 Kg per Ha). D-17 was the best parent in crosses and their S4XS4 progenies were of high yielding performance (Table 4), usually over 10000 Kg per Ha.

The criteria CV and CC are presented in Table 5. According to Fasoulas (1988, 1993), using the CC and CV criteria we showed that the most stable S-lines were D-17, G-33 and G-35, with relative CC% values (100, 45 and 36 respectively) and CV% (17, 19 and 22 respectively). Best hybrids D-17 X G-33, D-17 X G-22, D-17 X A-27, Lorena (PR3183) exhibited extra low CV values (9, 11, 10 and 10% respectively).

Productivity index *P*, pointed out that the most productive lines like D-17 and G-33 exhibit the greatest *P* values (Table 6). The two hybrids used as control had increased yield and *P* values, but one s-line cross D-17XG-33 reached their productivity, followed by the crosses of best performing line D-17 to G-22, D-27 and A-8 (Table 6). High yielding lines were found in best productive crosses (Table 7). Thus, lines D-17, A-8, A-27 contributed their

Table 3: S5 line mean yield in Kg per Ha, productivity index *P*, total (cumulative) and maximum (max) *P* values, and relative yield (%B73)

_	(/86/3)					
No	S-line	Mean	productivity index P	total <i>P</i>	max <i>P</i>	%B73
1	D-17	13000	91	269	53	500
2	A-8	11050	76	170	32	425
3	G-35	11000	72	52	21	423
4	G-33	10000	62	63	32	385
5	D-1	9750	62	47	21	375
6	B-35	8600	52	10	10	331
7	A-29	8600	52	74	53	331
8	A-27	7800	48	395	53	300
9	G-10	7800	48	99	37	300
10	B-14	6650	29	32	32	256
11	A-22	6500	19	42	37	250
12	D-8	6000	10	5	5	231
13	G-22	5200	5	116	42	200
14	D-5	5200	5	42	32	200
15	D-2	4800	0	26	21	185
16	A-2	4550	0	42	21	175
17	D-30	4150	0	31	21	160
18	B-24	4150	0	10	5	160
19	D-27	3900	0	36	26	150
20	G-27	3650	0	5	5	140
21	B-36	3250	0	26	21	125
22	B73	2600	0	53	32	100

LSD (0.05)= ±2300, CV%=28, General Mean = 6750

per se productivity in their crosses too, but in the last table Mid-parent heterosis and heterobeltiosis was low (Tables 6 and 7). Sometimes productivity of high yielding lines resulted in low or negative heterobeltiosis and Mid-parent heterosis found also low except some cases of crosses between lines with different S1/HS behaviour where heterosis was satisfactory (near 50%).

In Fig. 1, the level of productivity of lines and their crosses was presented in a bar scheme (first introduced by Greveniotis et al., 2009). Crosses were in a higher level and the most productive S-lines contributed in higher yield crosses, but not in crosses to common external parent B73. Main S-line relative yield progress from S1 to S7 figured out the most productive and stable lines across years (and generations) like lines D-17, or G-33 (Fig. 2).

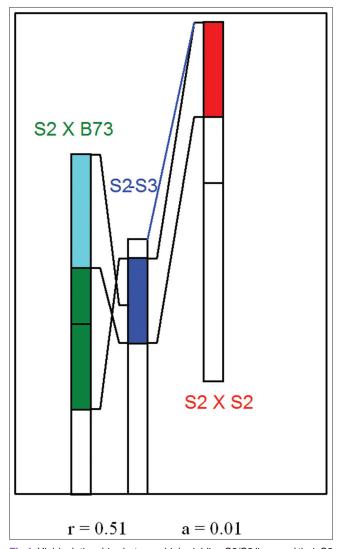


Fig 1. Yield relationships between high-yielding S2/S3 lines and their S2 crosses and crosses to B73. The contribution of yielding performance of S2, S3 lines to their crosses. Relative yield is presented schematically by colours, bars and lines of yielding performance level (the correlation coefficient r is also presented, statistically significant at 0.01 level).

Table 4: S4XS4 crosses in three RCBs (set 1, 2, 3) Mean yield in Kg per Ha, yield (%) of the mean control (mean of PR3183 and PR3165 yield) and productivity index P

No	Crosses set1	Mean	%	P	Crosses set2	Mean	%	P	Crosses set3	Mean	%	P
1	A-27 X G-22	5600	43	10	D-17 X G-22	14300	91	42	A-8 X D-5	10800	73	32
2	A-27 X G-35	8200	62	21	D-17 X G-35	11700	74.5	10	A-8 X B-14	10800	73	32
3	A-27 X G-33	8600	65.5	32	D-17 X G-33	12600	80	10	A-8 X A-10	4150	27.5	0
4	A-27 X G-27	2600	20	0	D-17 X G-27	10800	68.5	5	A-8 X B-29	8200	55.5	21
5	A-27 X B-24	5350	40.5	5	D-17 X B-24	9900	63	5	A-8 X D-8	4950	34	0
6	A-27 X D-27	3250	25	0	D-17 X D-27	11700	74.5	10	A-8 X G-22	10800	73	32
7	A-27 X G-5	9350	71	37	D-17 X G-5	11450	73	5	A-8 X A-2	8300	56	21
8	A-27 X G-10b	7800	59.5	21	D-17 X G-10b	12100	77	10	B-26 X G-27	6900	46.5	0
9	A-27 X B-36	2350	18	0	D-17 X B-36	11300	72	5	D-27 X G-10	10150	68.5	26
10	A-27 X D-1	8200	63	21	D-17 X D-1	8700	55.5	0	B-36 X D-1	9750	66	21
11	A-27 X D-2	8200	63	21	D-17 X D-2	10900	69.5	5	A-27 X D-17	11600	77.5	53
12	A-27 X G-10a	9350	71	37	D-17 X G-10a	10400	66	5	A-27 X A-8	4400	30	0
13	A-27 X B-35	3000	23	0	D-17 X B-35	11850	75	10	A-8 X D-17	10900	74.5	32
14	A-22 X D-30	7150	54.5	21	D-17 X D-30	12750	81	10	D-17 X A-27b	8300	56	21
15	A-27 X A-2	6500	50.5	21	D-17 X D-5	12500	79.5	10	G-35 X G-33	8600	58	21
16	A-27 X B73	7400	55.5	21	D-17 X B73	6000	38	0	A-8 X B73	4800	33	0
	PR3183	12350	94	95	PR3183	14450	92	42	PR3183	14450	98	89
	PR3165	14050	106	95	PR3165	17000	108	89	PR3165	15100	102	95
	Mean check		100		Mean check		100		Mean check		100	
	$LSD.05 = \pm 2800$				$LSD.05 = \pm 2850$				$LSD.05 = \pm 2900$			
	CV% = 24				CV% = 15				CV% = 18			
	General = 8600				General = 11700				General = 9600			

In general, S-line yield was improved and stabilized across years and selfing generations (Tables 3, 5, 6 and Fig. 2), contributing in high SXS crosses (Tables 2, 4, 5 and 6).

DISCUSSION

Maize yield is usually based in heterotic phenomena of heterozygote individuals that exhibit high yielding performance even under stress conditions (Duvick, 1992, 2005; Tollenaar & Wu, 1999; Ipsilandis & Vafias, 2005). Maize breeders balance between these main goals of breeding (yield, uniformity and stability) and the cost of developing parents to be used in the final product which is a high performance F1 hybrid (Vafias & Ipsilandis, 2005). In our study, the continuous selfing and per se evaluation led to high yielding lines, exhibiting homozygote vigour. High yielding lines may reduce hybrid production cost and is nowadays an important parameter for breeders (Fehr 1987). Best crosses in our study D-17 X G-33, D-17 X G-22, D-17 X A-27, Lorena (PR3183) exhibited extra low CV values. Fasoulas (1988, 1993) stated that stability is important as much productivity and CV may be a good criterion for stability behaviour. In many studies heterozygosity is accompanied by productivity and stability (Ipsilandis et al., 2006; Fasoula, 2009). It seems that dispersed heterozygous genes ensure a better balance in their genomes (Kearsey & Pooni, 1992; Duvick, 1992, 2005).

Table 5: S6 line per se and S5XS5 crosses productivity and stability according to the two criteria: CV and CC (relative combined criterion)

combined criterion)									
S6 Line	CV%	CC%	Crosses	CV%	CC%				
D-17	17	100	D-17 × G-33	9	98				
G-33	19	45	D-17 × G-22	11	88				
G-22	28	14	D-17 × D-27	17	47				
G-35	22	36	D-17 × A-8	14	51				
D-1	28	20	D-17 × G-27	24	27				
A-27	44	8	$D-17 \times B-24$	15	41				
G-10	32	12	A-27 X G-10	17	27				
D-30	22	9	A-27 X D-17	10	58				
D-8	38	6	D-17 X D-2	39	8				
D-2	22	10	A-8 X D-8	37	5				
A-8	50	6	A-27 X G-35	27	12				
A-2	36	3	D-17 X D-30	16	26				
G-27	31	3	A-8 X A-2	17	20				
B-24	48	2	A-27 X A-8	26	9				
D-27	24	4	A-27 X B-24	15	10				
B-36	43	1	A-27 X B-36	45	1				
-			A-27 X D-27	33	2				
-			A-27 X G-27	50	1				
В73	30	1	PR3183	10	100				
			PR3165	15	90				

In our study, selfing and *per se* evaluating led to high yielding S7 maize lines, a promising material to be used as parents for crosses (Ipsilandis, 1996). Their crosses to common foreign parent led to limited heterotic phenomena and relative low yielding performance. Heterobeltiosis was found near zero or

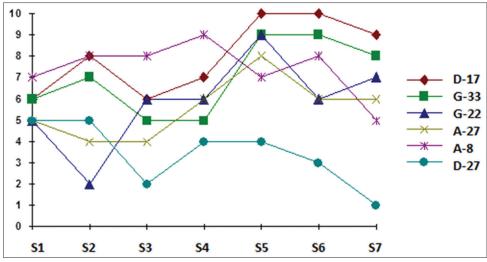


Fig 2. Main S-line relative yield progress from S1 to S7 (climax 1 to 10).

Table 6: S6 line yield per se in Kg per Ha, yield % of mean B73 control (%B73), crosses between S5 lines mean yield in Kg per Ha, yield % of mean of the two controls PR3183 and PR3165 (%MC) and yield % of PR3183 (%C)

No	S6 lines	Yield	Р	%B73	Crosses S5XS5	Yield	P	%MC	%C		
1	D-17 (1A)	10400	100	372	PR3165	16750	95	107	115		
2	D-17 (3)	8700	70	312	D-17 X G-33	14700	65	94	101		
3	D-17 (1)	8650	70	309	PR3183	14400	60	93	100		
4	G-33	8450	65	302	D-17 X G-22	14300	60	92	99		
5	G-22	7950	55	284	D-17 X D-27	14300	60	92	99		
6	G-35	7650	55	274	D-17 X A-8	14150	60	91	98		
7	D-1	6900	55	246	D-17 X G-27	13800	60	88	95		
8	A-27	6750	50	242	D-17 X B-24	12600	30	81	87		
9	G-10	6500	40	232	A-27 X G-10	11300	25	73	78		
10	D-30	5200	35	186	A-27 X D-10	10800	20	69	74		
11	D-8	5050	30	181	D-17 X D-2	10400	20	67	72		
12	D-2	4950	25	177	A-8 X D-8	10150	20	65	70		
13	A-8	4300	5	153	A-27 X G-35	10000	20	64	69		
14	A-2	3500	0	125	D-17 X D-30	9900	20	63	68		
15	G-27	3400	0	121	A-8 X A-2	9100	20	58	62		
16	B-24	3250	0	116	A-27 X A-8	8450	20	54	58		
17	B73a	3000	0	107	A-27 X B-24	6250	0	40	43		
18	B-36	2850	0	102	A-27 X B-36	4550	0	29	31		
19	D-27	2750	0	98	A-27 X D-27	4550	0	29	31		
20	B73b	2600	0	93	A-27 X G-27	4400	0	28	30		
	$LSD_{.05} = \pm 159$	0			$LSD_{.05} = \pm 2030$						
	CV% = 20				CV% = 13						
	General mean	n = 5600			General mean = 108	General mean = 10850					

negative, proving that such kind of parents cannot contribute in high yielding crosses because of the accumulation of useful additive alleles in one parent that are not favoured in heterozygote condition (Ipsilandis & Koutsika-Sotiriou, 2000). Fasoulas (1988, 1993) depicted the importance of extensive additive gene action for heritability and productivity, and additive gene action in our study was always present because of the proper per se selection of S-lines. Ipsilandis (1996) showed that this kind of selection may improve productivity of inbred lines, with positive impact on heritability and stability. Ipsilandis et al. (2006) recorded

various criteria for developing second-cycle hybrids in maize, exploring useful additive gene action. In our study, we used S1/HS for oriented crosses to a more reasonable basis by combining lines with different behaviour in per se and cross yielding performance. Differences in HS/S1 performance also affect the kind of gene action in developing final inbred lines (Ipsilandis & Koutsika-Sotiriou, 2000).

The three criteria used differences in heterobeltiosis, crosses to common parent and between S lines. Low heterobeltiosis is accompanied by high yielding performance of S-lines and

Table 7: S4XS4 cross yields % of controls in first year (A) of evaluation (A%), S5XS5 cross yields % of checks in second year (B) of evaluation (B%), mean of years (AM%), Mid-parent (MP) heterosis (%) in the two years (A and B) and total mean (MPA, MPB, MPM), heterobeltiosis (HB%) in the two years (A and B) and total mean (HBA, HBB, HBM)

Crosses	A%	В%	AM%	MPA	MPB	MPM	HBA	HBB	НВМ
High X High yielding S1									
D-17 X G-33	80	94	87	+10	+56	+33	-3	+41	+19
D-17 X A-8	75	91	83	-3	+93	+45	-10	+36	+13
High X Middle yielding S1									
D-17 X G-22	91	92	92	+57	+55	+56	+10	+38	+24
D-17 X D-2	69	67	68	+3	+36	+20	-16	0	-8
A-27 X G-35	62	64	63	+3	+39	+21	-13	+31	+9
A-8 X D-8	34	65	50	-37	+120	+41	-51	+100	+25
D-17 X A-27	77	69	73	+18	+26	+22	-5	+4	-0.5
A-8 X A-27	48	54	51	-50	+53	+1	-58	+25	-17
A-27 X G-10	71	73	72	+43	+69	+56	+43	+67	+55
High X Low yielding S1									
D-17 X D-27	74	92	83	+38	+118	+78	-10	+38	+14
D-17 X G-27	68	88	78	+30	+100	+65	-17	+33	+8
D-17 X B-24	73	81	77	+19	+85	+52	-21	+21	0
D-17 X D-30	81	63	72	+48	+27	+38	-2	-5	-3
A-8 X A-2	56	58	57	+13	+133	+73	-20	+112	+46
Middle X Low yielding S1									
A-27 X B-24	40	40	40	+6	+27	+16	-19	-6	-13
A-27 X B-36	19	29	24	-48	-3	-25	-63	-31	-47
A-27 X D-27	25	29	27	-33	-4	-19	-55	-33	-44
A-27 X G-27	20	28	24	-45	-13	-29	-60	-35	-47
Checks									
PR3165	106	107	106						
PR3183	94	93	94						
Mean check	100	100	100						

High > 8500 Kg per Ha *per se* yield of parent S lines Middle > 4800 and < 8500 Kg per Ha *per se* yield of parent S lines Low < 4800 Kg per Ha *per se* yield of parent S lines

crosses between these improved lines were generally high, but they based their productivity mainly on additive gene action and not heterozygotic superiority (Ipsilandis et al., 2005). Foreign common parent with poor per se performance lead to low yielding cross performance, proving that the basis of productivity of new crosses was depended mainly on favourable gene action (Ipsilandis et al., 2005). Per se evaluation increased line yield and resulted in crosses at satisfied yield level of productivity partly based on additive alleles possessing many homozygotic gene loci. Prognostic criteria of honeycomb methodology on parent lines involved Productivity index P, CV and CC. In our study CV proved to be a good criterion to estimate stability, but CC was a little confusing for the productivity of crosses, in comparison to S-lines where the most productive showed high CC values. Especially for crosses, the CC results were in disagreement to other criteria, like yielding performance, not revealing the most productive genotypes. Thus, CC was not a proper criterion for selecting crosses and it should be avoided. Productivity index P, although a difficult to use statistic, exhibited the superiority of the best lines. The top-yielding lines such as D-17, G-33 etc., showed high yields and simultaneously high P in all comparisons.

CONCLUSIONS

S1/HS comparisons were used for targeted crosses to by combining lines with different behaviour in per se and cross yielding performance. Differences in S1/HS performance also affect the kind of gene action in developing final inbred lines.

Selfing and *per se* yield evaluation led to high yielding S7 maize lines, a promising material to be used as parents for crosses. Their crosses to common foreign parent led to limited heterotic phenomena and relative low yielding performance. Heterobeltiosis was found near zero or negative, proving that such kind of parents cannot contribute in high yielding crosses because of the accumulation of useful additive alleles in one parent that are not favoured in heterozygote condition.

Crosses between improved lines developed by the certain procedure generally exhibited high yielding performance mainly based on additive gene action and not heterozygotic superiority. Foreign common parent, with relatively poor per se performance, lead crosses to low yielding performance, being an additional proof that the basis of productivity of new crosses was depended mainly on favourable additive gene action.

Prognostic breeding is more accurate when selection is applied for exploitation of additive gene action. CV proved to be a good criterion for stability estimations, but CC was confusing for estimating the productivity of crosses, being more accurate in case of S-lines where the most productive showed high CC values. Productivity index *P* exhibited the superiority of the best lines.

ACKNOWLEDGEMENT

Dedicated to the Greek breeder Apostolos Fasoulas.

REFERENCES

- Bauman, L. F. 1981. Review of Methods Used by Breeders to Development Superior inbreds. Proceedings of the 36th Annual Corn Sorghum Industry Research Conference. American Seed Trade Association, Washington, DC, pp. 199-208.
- Coors, J. G. 1988. Response to four cycles of combined Half-sib and S1 family selection in Maize. Crop Sci. 28: 91-896.
- Crow, J. F. 2000. The rise and the fall of overdominance. Plant Breed. Rev. 17: 225-257.
- Duvick, D. N. 1992. Genetic contributions to advances in yield of U.S. maize. Maydica. 37: 69-79.
- Duvick, D. N. 1996. Plant breeding, an evolutionary concept. Crop Sci. 36: 539-548.
- Duvick, D. N. 1999. Heterosis: Feeding people and protecting natural resources. In: Coors, J. G. and S. Pandey, (Eds.), The Genetic and Exploitation in Crops. American Society of Agronomy. Inc., Crop Science Society of America Inc., Soil Science Society of America Inc., Madison, WI.
- Duvick, D. N. 2001. Biotechnology in the 1930s: The development of hybrid maize. Nat. Rev. Genet. 2(1): 69-74.
- Duvick, D. N. 2005. Genetic progress in yield of United States maize (*Zea mays* L.). Maydica. 50: 193-202.
- Falconer, D. S. 1960. Introduction to Quantitative Genetics. 1st ed. Oliver and Boyd, London.
- Fasoula, V. A. 2008. Two Novel Whole-plant Field Phenotyping Equations Maximize Selection Efficiency. Proceedings of the 18th Eucarpia General Congress. Modern Cultivar Breeding for Present and Future Needs. Valencia, Spain, pp. 361-365.
- Fasoula, V. A. 2009. Selection of High Yielding Plants Belonging to Entries of High Homeostasis Maximizes Efficiency in Maize Breeding. Proceedings of the International Eucarpia Conference in Maize and Sorghum Breeding in the Genomics Era. Bergamo, Italy, p. 29.
- Fasoula-loannides, D. A. 1992. The Impact of Positive and Negativecompetition on Plant Domestication. International Conference Development of New Crops, Jerusalem, BG University.
- Fasoulas, A. C. 1981. Principles and Methods of Plant Breeding. Department of Genetics and Plant Breeding, Aristotelian University of Thessaloniki, Greece.
- 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. Department of Genetics and Plant Breeding, Aristotelian University of Thessaloniki, Greece.
- Fasoulas, A. C. 1993. Principles of Crop Breeding. Department of Genetics and Plant Breeding, Aristotelian University of Thessaloniki, Greece.
- Fehr, W. R. 1987. Principles of Cultivar Development. 1st ed. MacMillan Publishing Company, Ames, Iowa.
- Gomez, K. A. and Gomez, A. A. 1984. Statistical Procedures for Agricultural Research. John Wiley and Sons, Inc., New York.
- Goulas, C. K. and Lonnquist, J. H. 1976. Combined half-sib and S1 family selection in a maize composite population. Crop Sci. 16: 461-464.
- Greveniotis, V. and Fasoula, V. A. 2016. Application of prognostic breeding in maize. Crop Pasture Sci. 67: 605-620.
- Greveniotis, V., O. Xanthopoulou, E. Pessios, P. Deligeorgidis, D. Stefanis and C. G. Ipsilandis. 2009. Honeycomb evaluation of barley germplasm under pre-evaluated environments. Cereal Res. Commun. 37(4): 579-586.
- Greveniotis, V., E. Sioki and C. G. Ipsilandis. 2018. Estimations of fibre trait stability and type of inheritance in cotton. Czech J. Genet. Plant Breed. 54(4): 190-192.
- Greveniotis, V., S. Zotis, E. Sioki and C. G. Ipsilandis. 2019. Improving pedigree selection in applied breeding of barley populations. Cereal Res. Commun. 47(1): 123-133.
- Hallauer, A. R. 1979. Corn Breeding Opportunities in the 1980's.
 Annual Corn Iowa Seed Dealers Association. Des Moines.
- Ipsilandis, C. G. and M. Koutsika-Sotiriou. 2000. The combining ability of recombinant S-lines developed from an F2 maize population. J. Agric. Sci. (Cambridge). 134(2): 191-198.
- Ipsilandis, C. G., P. N. Deligeorgidis, L. Giakalis, M. Koutsika, A. Papadopoulou and V. Xanthopoulos. 2005. Breeding for homozygotic superiority and stability in maize without loosing combining ability. Asian J. Plant Sci. 4: 499-506.
- Ipsilandis, C. G. and B. N. Vafias. 2005. Plant density effects on grain yield per plant in Maize: Breeding implications. Asian J. Plant Sci. 4: 31-39.
- Ipsilandis, C. G., I. S. Tokatlidis, B. Vafias and D. Stefanis. 2006. Criteria for developing second-cycle hybrid in maize. Asian J. Plant Sci. 5: 680-685.
- Ipsilandis, K. 1996. The Possibility to Predict Combining Ability
 Between Maize Inbred Lines Based on Best Cross Performance.
 (Doctoral Dissertation), Aristotle University of Thessaloniki,
 Thessaloniki, Greece.
- Kearsey, M. J. and H. S. Pooni. 1992. The potential of inbred lines in the presence of heterosis. In: Dattee, Y., C. Dumas and A. Gallais, (Eds.), Reproductive Biology and Plant Breeding. Springer-Verlag, London, pp. 371-386.
- Koutsika-Sotiriou, M. and I. Bos. 1996. Heterosis after several numbers of cycles of mass honeycomb selection in maize. J. Genet. Breed. (Italy). 49: 361-368.
- Koutsika-Sotiriou, M. 1985. Improving Combining and Yielding Ability of Maize (*Zea mays L.*). (Doctoral Dissertation), Aristotle University of Thessaloniki, Thessaloniki, Greece.
- Smith, O. S. 1984. Comparison of effects of reciprocal recurrent selection in the BSSS(R), BSCB1(R) and BS6 population. Maydica. 24: 1-8.
- Tollenaar, M. and J. Wu. 1999. Yield improvement in temperate maize is attributable to greater stress tolerance. Crop Sci. 39: 1597-1604.
- Tollenaar, M., A. Ahmadzadeh and E. A. Lee. 2004. Physiological basis of heterosis for grain yield in maize. Crop Sci. 44: 2086-2094.
- Vafias, B. N. and C. G. Ipsilandis. 2005. Combining ability, gene action and yielding performance in maize. Asian J. Plant Sci. 4: 50-55.