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A Triple Stress Effect on Monogenotypic and Multigenotypic Maize Populations

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Abstract: The purpose of this study was to evaluate the yielding performance of maize under stress conditions involving mixing of different genotypes, plant density and low water/fertilizer inputs. The impact on yield from competition and genetic differences was analysed. Two F1 hybrids (Prisma and Funo) were used, their F2s, the mixture of the F2s and the F1+F2 mixture of the first hybrid, in a high and in a low-inputs experiment. The two F1 hybrids increased field yield until 133300 plants ha^{-1} and at 190000 plants ha^{-1} there was a decrease due to increased rate of declining individual plant yield. The rate of decrease of individual plant yield is a parameter that determines the final field yield realised under increasing plant densities. In full-inputs experiment, there was a significant interaction between genetic materials and plant densities, meaning that different materials respond in a different way under the stress of density. F2 generations were affected lesser than F1 hybrids. Genetic purity proved to be a greater stress condition than density effects. This was more apparent in the low-inputs experiment where differences between genetic materials were much more significant and plant density was a limited stress, almost eliminated by the stronger stress of lower inputs. The low-inputs condition is a major stress masking the effects of plant density. F1 yield in the low-inputs experiment was close to the F2 yielding performance in the full-inputs experiment. Higher plant densities showed lower inbreeding depression values for both hybrids in both experiments. This was due to F2s buffering, resulting in increased relative yield in comparison to the F1s. The increasing plant density resulted in increasing CV values and number of barren plants. Extreme conditions, such as plant density and low inputs, showed that the F1s are affected more than multigenotypic materials, exhibiting greater increase in CV values. F1 hybrid Funo, showed increased numbers of barren plants and this may be an indication of low seed purity, but indications from F1 Funo and Prisma yield comparisons and from F1/F2 comparisons, showed that even if there was a quantity of impure seed partition for hybrid Funo this was small. Low inputs resulted in significant soil heterogeneity, maybe stronger as a stress condition than plant density effects and allocompetition. Ranking stress conditions, low inputs is the most severe stress because of the increased needs of modern maize hybrids, followed by seed purity and soil heterogeneity. Plant density is a problem only under extremely high or low populations.

Key words: Plant density, maize, competition, low-inputs, yield

INTRODUCTION

The contribution of maize breeding on hybrid yield per plant is summarized in Duvick's findings (1997), that during the past 70 years, breeding had no effect on hybrid yield per plant improvement, as it was estimated under low stress conditions (1 plant m^{-2}). On the other hand, breeding in maize has contributed to improvement of hybrid yield per unit area (Troyer, 1995; Duvick, 1997), when hybrid grain yield was estimated at the typical plant density of 7.9 plants m^{-2}. This results indicated that higher grain yield productivity of modern maize hybrids resulted indirectly by improving tolerance to various biotic and abiotic stresses and by improving the efficiency of capture and use of resources (Derieux *et al*., 1987; Russell, 1991; Tollenaar and Wu, 1999).

Differences in response to stresses between older and newer hybrids has been shown for various conditions such as: low soil moisture in the field (Dwyer *et al*., 1992; Nissanka *et al*., 1997), low soil N (McCullough *et al*., 1994), weed interference (Tollenaar *et al*., 1997) and high plant population density (Duvick, 1984; Bonan, 1991;

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Tollenaar, 1992; Vafias *et al*., 2000a, 2006; Ipsilandis *et al*., 2005). To overcome density effects in farmer's field Fasoula and Fasoula (1997a, b, 2000) emphasised the importance of low stress conditions in optimising the effectiveness of selection for new cultivars, aiming in improved potential yield per plant, tolerance to stresses and responsiveness to inputs. Plant density in farmer's field is considered an important stress factor since, in such conditions, competition between different genotypes is very strong (Fasoulas, 1981, 1988, 1993; Daynard and Muldoon, 1983; Tetio-Kagho and Gardner, 1988; Bonan, 1991; Thomas *et al*., 1994; Vafias *et al*., 2000b). Optimum plant density for some maize hybrids was found between 70,000 and 100,000 plants ha^{-1} (Vafias *et al*., 2000b, 2006) indicating density dependence of maize hybrids (Tokatlidis, 2001; Tokatlidis *et al*., 2001).

The present study was based on a triple stress for two maize hybrids, including plant density for analysing yielding performance, mixing of different genotypes for analysing competition and genetic purity effects and low inputs to depict the most significant stress conditions.

MATERIALS AND METHODS

In year 2000, in the experimental farm of Technological Education Institute of Larissa, Greece, two experiments were conducted. The first (full-inputs experiment) was based on the availability of fertilizer (about 24 units of N) and irrigation. The second (low-inputs experiment) was based on lack of fertilizer (about only 10 units of N) and irrigation (half the water given in the first experiment).

The genetic materials used were the F1 generations of commercial maize hybrids Prisma and Funo, the F2 generations of the two hybrids, the balanced mechanical mixture F1+F2 of hybrid Prisma and the balanced mechanical mixture of the F2 generations of the two hybrids (F2+F2 Prisma and Funo). The plant densities used in both experiments were 53,300, 66,600, 88,800, 133,300 and 190,000 plants ha^{-1} (plants ha^{-1}).

The experimental design was based on a complete blocks design, with four replications of each treatment. The two factors (plant densities and genetic materials) were arranged in a split-plot design. The main factor (genetic materials) formed the subplots and the second factor (plant densities) formed the main plots. Each plot consisted of double rows, 5 m long and 75 cm row to row spacing. Plants on the rows were sown on the proper distances (25, 20, 15, 10 and 7 cm) to form plant densities. Factorial analysis was based on Snedecor and Cochran (1980). Yield estimation was based on individual plant yield in grammars (g) and field yield in kg per hectare. Humidity was found below 15%. Coefficient of Variation (CV%), followed by Q-Q plots analysis and barren plants (%) were also calculated. Inbreeding depression (%) estimation was calculated according to the formula: ID(%) = 100(1-F2/F1).

RESULTS

In the full-inputs experiment, F1 hybrid Prisma yielded better than other materials (Table 1), increasing field yield from lower to higher plant densities until the optimum of 133300 plants ha^{-1} was reached (from 12980 to 20500 kg ha^{-1}). The rest of the genetic materials showed almost the same behaviour (Table 1). The F2 mixture (Prisma+Funo), was the lowest yielding material in low plant densities, but in higher densities overyielded F2 Funo and reached yield of F2 Prisma. 133300 plants ha^{-1} was the optimum plant density for all materials and especially for F1 Prisma (Fig. 1a). Concerning yield, significant interaction was found between the two factors

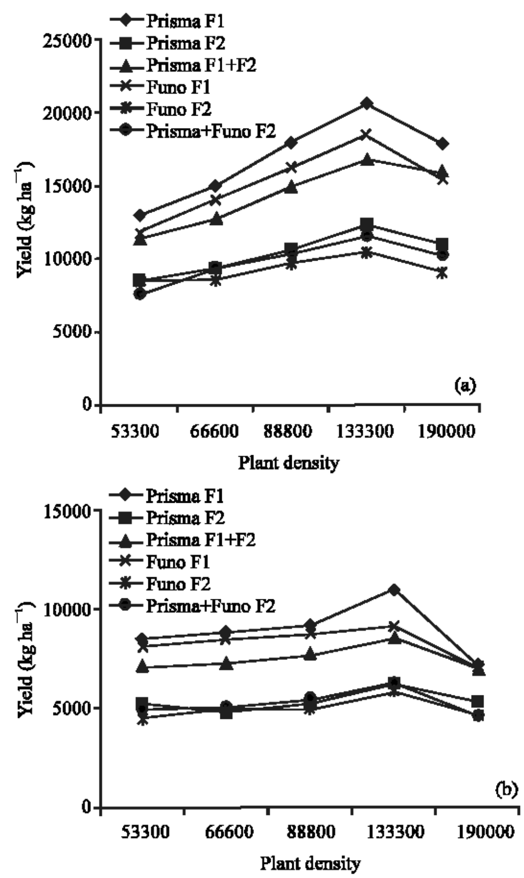

Fig. 1: Field yield in kg ha^{-1}, across plant densities for the six genetic materials (a = full inputs, b = low inputs)

Table 1: Measurements for estimation of field yield in kg ha^{-1}, individual plant yield in g per plant, Coefficient of Variation (CV%) and percentage of barren plants (%), across five plant densities (53300, 66600, 88800, 133300 and 190000 plants ha^{-1}) for high inputs field, including F1s and F2s of commercial hybrids Prisma and Funo, mixture from F1 and F2 from Prisma and mixture from F2s of Prisma and Funo

		Prisma			Funo		Prisma+Funo
Plant density	Measurement	F1	F2	F1+F2	F1	F2	F2
53300	kg ha^{-1}	12980	8480	11380	11780	8370	7650
	g per plant	243	159	213	221	157	143
	CV%	17	46	32	16	34	42
	Barren plants%	0	0	0	0	3	7
66600	kg ha^{-1}	14880	9330	12720	13980	8600	9360
	g per plant	223	140	191	210	129	140
	CV%	23	43	37	20	43	35
	Barren plants%	2	7	12	2	6	7
88800	kg ha^{-1}	17850	10580	14870	16160	9640	10340
	g per plant	201	119	167	182	108	116
	CV%	29	54	44	26	42	49
	Barren plants%	3	14	19	3	10	15
133300	kg ha^{-1}	20500	12290	16790	18380	10430	11540
	g per plant	154	92	126	138	78	87
	CV%	31	40	51	28	43	50
	Barren plants%	4	26	23	4	30	27
190000	kg ha^{-1}	17790	10930	15860	15430	9030	10250
	g per plant	94	58	83	81	48	54
	CV%	46	56	43	40	58	55
	Barren plants%	16	41	34	17	44	43

Statistically significant differences (for yield estimations) were found between different genetic materials and plant density levels, at $p<0.001$ and interaction between the two factors, at $p<0.01$ (CVexp = 8.5%, MSerror = 0.6)

(genetic materials and plant density). Inbreeding depression for F1 hybrid Prisma was estimated at 0.35 in low plant density and 0.40 at optimum plant density. Inbreeding depression for F1 hybrid Funo was estimated at 0.29 in low plant density and 0.43 at optimum plant density. In 88800 plants ha^{-1} (farmer's field) inbreeding depression was almost the same for the two F1 hybrids (0.40-0.41). The individual plant yield was decreasing as plant density was increasing (Table 1), but the decreasing rate was slow until 133300 plants ha^{-1} and allowed higher field yield (Fig. 2a). At this density level the decreasing rate of individual plant yield became rapid, leading to lower field yield.

The CV(%) values were increasing as plant density increased for F1 hybrids (Table 1). F2 generations were more stable and in some cases CVs became lower at higher plant densities (Fig. 3a). Almost the same behaviour was found for mixtures. F1 CVs were in general lower than CVs of other materials but in higher plant densities the CVs were high and near to each other. Barren plants increased as plant density increased (Fig. 4a). The F1s showed lower barren plants than other materials (Table 1), especially in high plant densities. The increasing rate for F1s became apparent at 133300 plants ha^{-1}, while for the rest materials this was found at lower densities (usually 88800 plants ha^{-1}).

In the low-inputs experiment, F1 hybrid Prisma yielded better than other materials (Table 2), increasing field yield from lower to higher plant densities until the optimum of 133300 plants ha^{-1} was reached. Prisma F1+F2 was almost the mean of F1 and F2 separately and all the F2s exhibited the same performance (Table 2, Fig. 1a). All yields were lower than the first experiment (Full-inputs)

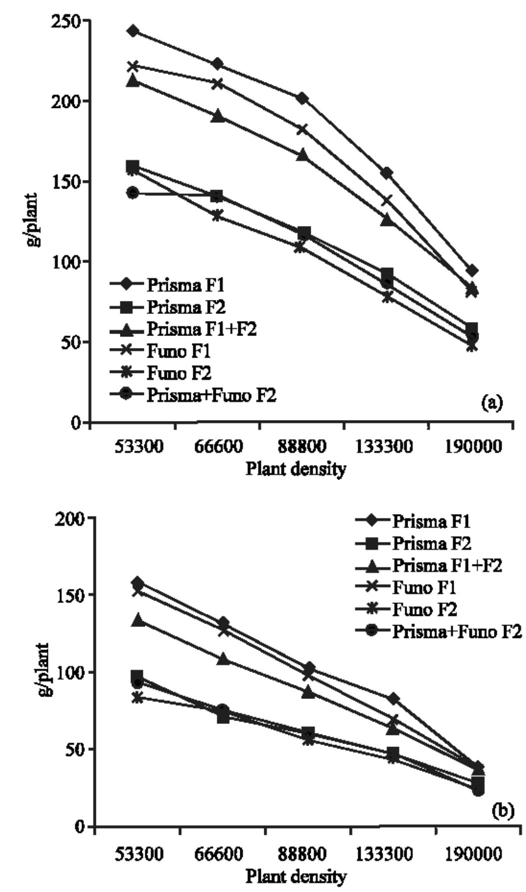

Fig. 2: Yield of individual plants in (g ha^{-1} plant, across plant densities for the six genetic materials (a = full inputs, b = low inputs)

Table 2: Measurements for estimation of field yield in kg ha^{-1}, individual plant yield in g per plant, Coefficient of Variation (CV%) and percentage of barren plants (%), across five plant densities (53300, 66600, 88800, 133300 and 190000 plants ha^{-1}) for low inputs field, including F1s and F2s of commercial hybrids Prisma and Funo, mixture from F1 and F2 from Prisma and mixture from F2s of Prisma and Funo

		Prisma			Funo		Prisma+Funo
Plant density	Measurement	F1	F2	F1+F2	F1	F2	F2
53300	kg ha^{-1}	8430	5150	7130	8080	4480	4950
	g per plant	158	97	134	152	84	93
	CV%	26	56	51	22	37	47
	Barren plants%	1	3	3	1	19	8
66600	kg ha^{-1}	8820	4820	7250	8480	4910	5060
	g per plant	132	72	109	127	74	76
	CV%	32	46	47	29	49	42
	Barren plants%	3	25	14	4	21	17
88800	kg ha^{-1}	9200	5310	7750	8720	4950	5460
	g per plant	103	60	87	98	56	61
	CV%	58	64	57	46	49	54
	Barren plants%	5	38	20	4	35	41
133300	kg ha^{-1}	10950	6240	8590	9140	5820	6250
	g per plant	82	47	64	69	44	47
	CV%	52	58	53	46	48	57
	Barren plants%	15	38	45	16	42	40
190000	kg ha^{-1}	7150	5360	7000	7010	4680	4630
	g per plant	38	28	37	37	25	24
	CV%	80	70	71	51	52	70
	Barren plants%	34	50	45	35	61	60

Statistically significant differences (for yield estimations) were found between different genetic materials, at $p<0.001$ and only for high density level, at the limit of $p = 0.0501$ (CVexp = 13.5%, MSerror = 0.4)

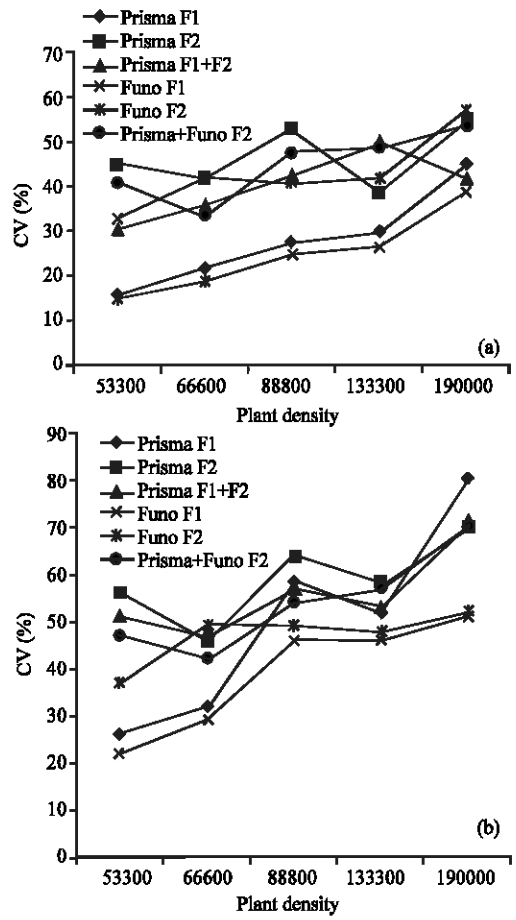

Fig. 3: Coefficient of Variation (CV%), across plant densities for the six genetic materials (a = full inputs, b = low inputs)

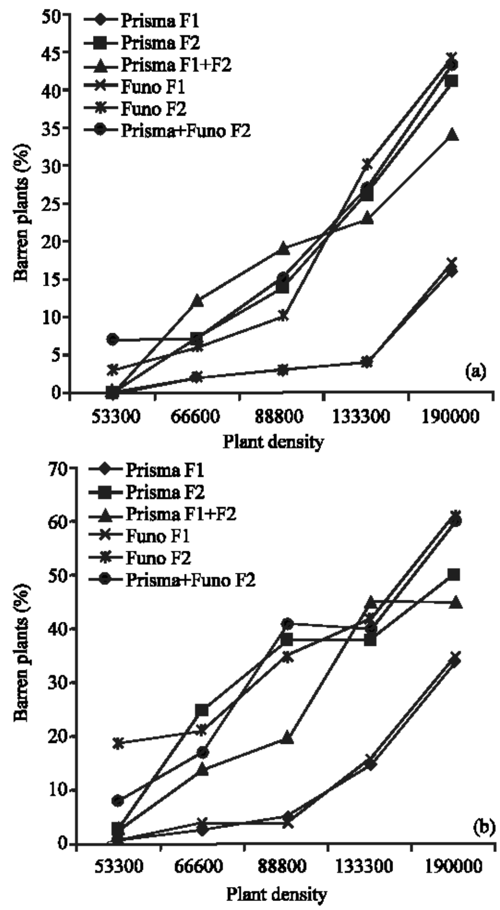

Fig. 4: Percentage of barren plants (%), across plant densities for the six genetic materials (a = full inputs, b = low inputs)

and the same was found for individual plant yield (Table 1 and 2; Fig. 1 and 2). Concerning yield, differences were found between all genetic materials and only for high density level (p = 0.05).

Inbreeding depression was estimated biased and found higher than the first experiment except for higher densities, where for Prisma was found at 0.25 instead of 0.39 and for Funo at 0.33 instead of 0.41. The CV values were increased in comparison to the first experiment (Table 1 and 2). Funo, in general (F1 and F2) exhibited lower or more stable CVs than other materials (Fig. 3b). Prisma CV values increased as plant density increased (Fig. 3b). Barren plants increased dramatically as plant density increased (Fig. 4b). The pure F1 hybrids exhibited lower numbers of barren plants and the rest of materials exhibited almost the same numbers of barren plants from 88800 to 133300 plants ha^{-1}, with an exception of Prisma F1+F2 mixture, especially at highest density (Fig. 4b).

DISCUSSION

Modern maize hybrids tolerate increased plant densities that contribute to higher field yields Duvick (1992). In the present study, the two F1 hybrids increased field yield until 133300 plants ha^{-1} and at 190000 plants ha^{-1} there was a decrease due to increased rate of declining individual plant yield. The rate of decrease of individual plant yield is an important parameter that determines the final field yield realised under increasing plant densities (Vafias *et al*., 2006). In full-inputs experiment, there was a significant interaction between genetic materials and plant densities, meaning that different materials respond in a different way under the stress of density. F2 generations were affected lesser than F1 hybrids. Mixtures of genotypes are not preferred for farmer's field because of lower yields due to competition effects (Fasoulas, 1988) although they exhibit advantages in controlling diseases or used for adaptation in extreme environments. Additionally, mixtures exhibit buffering under density stress in a way that F2 generations or F1/F2 mixtures are affected lesser than pure hybrids (Vafias *et al*., 2006). In general, mixtures of multigenotypic varieties, such as F2s, are not preferable due to their low yielding performance. Alternatively, mixtures of F1s of modern hybrids may exhibit a high and stable performance under various conditions due to proper breeding and in such cases it is possible that allocompetition is not a stronger stress factor than isocompetition in modern maize hybrids (Vafias *et al*., 2006). This may be true even for their F2s, since the F2 mixture of the two different hybrids showed a yielding performance almost equal to the mean of the two F2s separately indicating low allocompetition effects. Both genotype mixing and plant density proved to be significant stresses and in agreement with the findings reported by Fasoulas (1981, 1988, 1993), Vafias *et al.* (2000a) and Ipsilandis *et al.* (2005). On the other hand, genetic purity proved to be a greater stress condition than density effects and in agreement with the findings reported by Ipsilandis *et al.* (2005). This was more apparent in the low-inputs experiment where differences between genetic materials were much more significant and plant density was a limited stress, almost eliminated by the stronger stress of lower inputs. In the second experiment, only the F1s of the two hybrids exhibit significant changes in field yield: There is an increase until the 133300 plants ha^{-1}, but at 190000 plants ha^{-1} they exhibit significantly low yields, lower even from yields in 53300 plants ha^{-1}. In all other cases, the low-inputs condition is a major stress masking the effects of plant density. In general, F1 yielding performance in the low-inputs experiment was close (and sometimes lower) to the F2 yielding performance in the full-inputs experiment. Higher plant densities showed lower inbreeding depression values for both hybrids in both experiments. This was due to F2s buffering, resulting in increased relative yielding performance in comparison to the F1s. In other words, the percentage of increasing or decreasing performance, is always better (greater or lower, correspondingly) for F2s than for F1s. For this reason, authors suggest estimation of inbreeding depression in relatively low plant densities, where individual plants express better their yielding performance (Fasoulas, 1988).

The increasing plant density resulted in increasing CV values and number of barren plants. This was expected, since density effects lead to greater variability and decreased productivity. Extreme conditions, such as plant density and low inputs, showed that the F1s are affected more than multigenotypic materials, exhibiting greater increase in CV values. The percentage of barren plants may be an indirect estimation of original hybrid seed low purity (Vafias *et al*., 2000a). In the present study F1 hybrid Funo, showed increased numbers of barren plants and this may be an indication of low seed purity. On the other hand, the problem of improper seed production has an impact on field yield. Expected mean yield of maize hybrids in Greece equals mean yield found after multisite screening (≈12000 kg ha^{-1}) minus the approximate quantity 100 kg ha^{-1} x Inbred line percentage (%), for inbred line presence >10% (Ipsilandis *et al*., 2005). Our indications from F1 Funo and Prisma yield comparisons and from F1/F2 comparisons, showed that even if there was a quantity of impure seed partition for hybrid Funo this was small (<10%). Newer reports refer that, problems caused by genetic impurity may be overcome by increasing plant density (Vafias *et al*., 2000a) and this may be one of the reasons for better performance of modern maize hybrids under high density conditions.

Analysing experimental block differences (from ANOVA), there was found soil heterogeneity effects only in low-inputs experiment, which are considered to be more significant in low density (great plant to plant distance) and poor field conditions (Fasoulas, 1981, 1988). Thus, low inputs resulted in significant soil heterogeneity, maybe stronger as a stress condition than plant density effects and allocompetition.

Many researchers stated that field yield per unit area of maize hybrids (the hybrid dependence on plant density) and the competition impact on plant-to-plant variability, as well as the following consequences on maize breeding strategy constitute the key in the development of cultivars characterised by high and stable yield per unit area. Our research depicted the importance of proper seed production resulting in genetic purity of hybrid seed to be used in farmer's field. Reduced soil heterogeneity and high inputs may overcome problems from density effects and competition. For breeders and farmers, the balance between high (accompanied by competition) and low plant densities (accompanied by soil heterogeneity) must be attentively determined. Ranking stress conditions, it seems that low inputs is the most severe stress because of the increased needs of modern maize hybrids, followed by seed purity and soil heterogeneity. Plant density is a problem only under extremely high or low populations.

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