Asian Journal of
Plant Sciences

Comparative Analysis of Two Crop Yield Potential Models Based on Yield Potential per Plant of Maize and Bread Wheat Genotypes

[1]Ioannis S. Tokatlidis and [2]Ioannis T. Tsialtas
[1]Department of Agricultural Development, Democritus University of Thrace, Pantazidou 193,
Orestiada 68200, Greece
[2]National Agricultural Research Foundation, Cotton and Industrial Plants Institute, 57400, Sindos, Greece

Abstract: Crop yield potential assessment under a single density, assumed as optimum for maximum yield per unit area, might lead to biased judgment due to genotype by density interactions. Two models emphasizing yield per plant in the absence of competition (i.e., yield potential per plant), were applied in maize (*Zea mays* L.) and wheat (*Triticum aestivum* L.) genotypes to assess crop yield potential. The first model distinguishes crop yield potential into two components, yield potential per plant and tolerance to density, predicted through linear regression of yield per plant over a range of densities. The second model proposes three components, which are yield potential per plant, tolerance to stresses and responsiveness to inputs, determined in the absence of competition. Genotypes suggested by the models as the most promising were different than those depicted on the basis of the experimental data. Both models favoured genotypes characterized by improved yield potential per plant and being less density-dependent. Nevertheless, the two components of the first model were negatively associated. The first model determines the key parameter (i.e., yield potential per plant) indirectly, accuracy of which depends on the lowest density used. The second model assesses yield potential per plant in a direct way and seems to consider crop yield potential in a more integrated manner, whereas appears to represent an integral part of whole breeding approach.

Key words: Absence of competition, responsiveness to inputs, tolerance to stresses

INTRODUCTION

Crop yield potential of a cultivar is defined as its grain yield per unit area when grown in environments to which it is adapted, in other words under optimal environmental conditions (Evans and Fischer, 1999). Maize hybrids and wheat cultivars respond to plant density changes in a curvilinear manner (Tollenaar and Wu, 1999; Sangoi *et al.*, 2002; Lloveras *et al.*, 2004) and maximum grain yield per unit area is achieved at a narrow spectrum of plant densities (i.e., optimum density). Therefore, crop yield potential of a given genotype is assumed to represent its grain yield per unit area under its optimum density. However, because different genotypes may differ for optimum density (Berzsenyi and Dang, 2006; Sarlangue *et al.*, 2007), comparative evaluation of them under a single plant density might lead to biased judgment. Evans and Fischer (1999) noted: the absence of agreement on yield potential's definition and measurement can lead to misunderstanding as well as to misleading claims. Research in Europe and the USA indicated that interference between plots in cultivar trials

can distort yield and result in misleading conclusions from yield comparisons (Clarke *et al.*, 1998). Two models were proposed to assess the crop yield potential, both of which place particular emphasis on the yield potential per plant in the absence of competition (i.e., plant density is so low that there is no interplant interference of competition within the crop stand). The models suggest the single-plant yield instead of the usually used yield per unit area as the determinant parameter for crop yield potential measurement.

Yan and Wallace (1995) suggested a model (referred downward as first model) that distinguishes two components of crop yield potential: (i) the yield potential per plant and (ii) the tolerance of the single plant yield to plant density changes (i.e., tolerance to the scarcity of the limiting resources). Crop yield potential is more dependent on the yield potential per plant rather than on the density tolerance. Assessment of these components requires data from a range of different plant densities and is analyzed as follows. The crop yield per unit area (Y_c) is expressed as the product of established plants per unit area (the plant

Corresponding Author: Ioannis S. Tokatlidis, Department of Agricultural Development, Democritus University of Thrace,
Pantazidou 193, Orestiada 68200, Greece Tel: 0030 25520 41152 Fax: 0030 25520 41191

population density, D) and the mean yield per plant (Y_p) in the stand: $Y_c = DY_p$. A negative relationship between yield per plant and plant density exists, expressed by the equation: $Y_p = \alpha - bD$ where α and b are constants for a given genotype under a given environment. Intercept α represents a measure of the expected yield potential per plant. Slope b is the yield per plant sensitivity to changes in the plant density. Expected crop yield potential (Y_{pot}) of a given genotype can be determined by the product of the square of the expected yield potential per plant (α^2) of that genotype multiplied by its tolerance to increasing plant density (b^{-1}): $Y_{pot} = (1/4) \, \alpha^2 b^{-1}$. This equation denotes that in order the goal of high crop yield potential to be achieved, either improved yield at the single-plant level or tolerance to increasing plant density are desirable.

The second model proposed by Fasoula and Fasoula (2002) distinguishes three components of crop yield potential, all measured under a single ultra-low density so that any plant-to-plant interference for environmental inputs is minimized (i.e., absence of competition): (i) The first component is yield potential per plant, measured directly by the entry mean ($\overline{X}$). Improved yield potential per plant expands the lower limit of the optimum density range. (ii) The second component is tolerance to overall biotic and abiotic stresses, predicted by the standardized entry mean ($\overline{X}\sigma_p^{-1}$), that is the inverse value of coefficient of variation (CV). Tolerance to stresses improves tolerance to increased density, pests and drought and hence, reduces CV of single-plant yields by ensuring minimal plant-to-plant interference with equal sharing of resources. Improved standardized entry mean expands the upper limit of the optimum density range. (iii) The third component is responsiveness to inputs, predicted by the standardized entry selection differential ($(\overline{X}_s - \overline{X})\sigma_p^{-1}$). Genotypes carrying genes for responsiveness to inputs are capable to exploit improved growing conditions and this capacity is reflected on genotype's selection differential. Thus, improved standardized entry selection differential denotes adaptability to increasing environmental resources. A given genotype is assumed to have incorporated genes for advanced crop yield potential when combines high values for each particular component. Early generation selection at ultra-low density, on the basis of the three crop yield potential components, is a better strategy than selection in bulks, as it avoids the confounding effect of competition between distinct genotypes, leading to varieties characterized as density-independent and expected to be promising for improved crop yield potential (Fasoula and Fasoula, 2002).

In the work relative crop yield potential of maize and wheat genotypes is assessed according the aforementioned two models. The results are discussed in relevance with maximum yield per unit area obtained experimentally and the models are comparatively criticized.

MATERIALS AND METHODS

To achieve the goal data from previous studies conducted in Greece were used (1993-99 for maize and 1998-2003 for wheat) and therefore methods to achieve the materials are given briefly. Since comparative analysis of the two models was sought, this work includes only genotypes for which data under either a range of densities (for the first model) or an ultra-low density (required for the second model) were available. Ultra-low densities used were 0.74 and 1.2 plants m^{-2}, since these are assumed to approximate absence of competition for maize and wheat genotypes, respectively, according to Fasoulas (personal communication) who suggested absence of competition as a prerequisite to ensure selection effectiveness (Fasoulas and Fasoula, 1995).

Maize genotypes: Three experimental single-cross hybrids and two commercial single-cross hybrids (PR 3183 and B73xMo17) constituted the maize material. Honeycomb single-plant selection (Fasoulas and Fasoula, 1995) within F_2 generation of PR 3183 under the ultra-low density of 0.74 plants m^{-2} led to two S_5 parental lines and by random matings between plants of the two parental lines $S_5 \times S_5$ recycled hybrids were obtained (Tokatlidis *et al.*, 1998). Three $S_6 \times S_6$ recycled hybrids (named 1, 2, 3), advanced from the three $S_5 \times S_5$ hybrids that had the highest mean yield per plant and were significantly superior over their original hybrid at the ultra-low density of 0.74 plants m^{-2}, were the experimental hybrids of the present study (Tokatlidis *et al.*, 2001).

Wheat genotypes: Honeycomb single plant selection under the ultra-low density of 1.2 plants m^{-2} within a bread wheat cultivar (cv. *Nestos*) led to 20 first generation families. Six out of the 20 families (coded as H2, H4, H7, H8, H10, L8), along with their original cv. *Nestos*, constituted the wheat material. These families had exhibited the highest mean grain yields per plant under the aforementioned ultra-low density and-family L8 excepted-were significantly superior over that of the original cultivar (Tokatlidis *et al.*, 2006).

Crop yield potential assessment at a range of densities by the first model: The three experimental maize hybrids, along with their original hybrid PR 3183 and the check

hybrid B73xMo17, were evaluated in two locations for two years under the densities of 2.5, 4.2 and 8.3 plants m^{-2} (Tokatlidis, 2001). Density of 8.3 plants m^{-2} approximates the typical density used for late-maturing hybrids in Greece. The experimental design was a Randomized Complete Block (RCB) experiment, with three replications per hybrid and density. Each plot was harvested separately and the mean grain yield per hectare (ha) was computed at the 15.5% grain moisture level.

Concerning the seven wheat genotypes, experimentation at four densities (100, 300, 500, 700 plants m^{-2}) in two locations and for two years was conducted (Tokatlidis *et al.*, 2006). Entries were arranged according to the two-factor split-plot completely randomized blocks, where densities constituted the main plots and genotypes the subplots and four replications per entry and density were applied. Each subplot was harvested separately and mean grain yield per ha was determined at the 12% grain moisture level.

Data from both categories of materials were converted at the single-plant level (mean yield per plant). The expected yield potential per plant (α) and crop yield potential (Y_{pot}) of entries were estimated through intercept α and slope b of the linear regression analysis of yield per plant in grams over plant density in plants m^{-2} ($Y_p = \alpha$-bD), with Y_{pot} being equal to $(1/4) \alpha^2 b^{-1}$.

Crop yield potential assessment at an ultra-low density by the second model: The three recycled maize hybrids and their original hybrid PR 3183, were evaluated in a R-61 replicated honeycomb trial (Tokatlidis *et al.*, 1998), while data regarding the performance of the check hybrid B73xMo17 were obtained from an R-43 replicated trial conducted in the same location (Tokatlidis, 2000), both trials under the density of 0.74 plants m^{-2}. The six derived wheat families and their original cv *Nestos*, were tested in two R-21 replicated honeycomb trials at the density of 1.2 plants m^{-2} (Tokatlidis *et al.*, 2006).

Plants were harvested individually and the three crop yield components were computed by the HONEY microcomputer program (Batzios and Roupakias, 1997): yield potential per plant by the mean grain yield per plant $\overline{X}$, tolerance to stresses by the standardized entry mean $\overline{X}\sigma_p^{-1}$ and responsiveness to inputs by the standardized selection differential $(\overline{X}_s-\overline{X})\sigma_p^{-1}$. Each component value of a given entry, divided by the respective value of the check entry (hybrid B73xMo17 in case of maize and cv *Nestos* for wheat), constituted the component index for this particular entry. The three component indexes of each entry were added and ended up in a single value (i.e., combined index) representing the entry's crop yield potential index (Y_{ci}).

RESULTS AND DISCUSSION

As far as grain yield per unit area is concerned, curvilinear responses of maize and wheat genotypes to density changes are depicted in Fig. 1 (those of wheat families H4 and H7 are not shown). At the highest density of 8.33 plants m^{-2} (Y_{obt}), that approximates densities used by farmers in Greece for maize, hybrids PR 3183 and B73xMo17 yielded by around 2-7% higher than the three recycled hybrids, being significantly superior over the recycled hybrid 3 (Tokatlidis, 2001). Hybrid B73xMo17, that according to image of Fig. 1 showed an almost linear regression on plant density, seems to be capable of exploiting even higher densities, giving thus maximum crop yield well above the highest yields in the test. Maximum grain yield value (Y_{max}) derived from the parabolic response curve of hybrid B73xMo17, that was by 15% higher than its Y_{obt} value and by >18% higher in comparison with Y_{max} values of the recycled hybrids, is indicative. Therefore, one based on the experimental data depicted in Fig. 1 could assume that hybrid B73xMo17 has the highest crop yield potential. On the other hand, lines of the recycled hybrids demonstrate that their maximum grain yield per unit area is achieved at the density of approximately 6 plants m^{-2}, remaining constant even when density is higher than 8.33 plants m^{-2}. Optimum densities were found to be 6.1, 6.6 and 6.5 plants m^{-2} for recycled hybrids 1, 2 and 3, respectively and 8.5 and 10 plants m^{-2} for hybrids PR 3183 and B73xMo17, respectively, revealing strong genotype by density interaction (Tokatlidis, 2001). Considering graphs of wheat genotypes it is obvious that optimum density for both families and their original cv *Nestos* was around 500 plants m^{-2}. At that density family H10 exhibited the highest mean grain per unit area and was by about 9-11% significantly superior over families H2, H4, H8 and cv *Nestos* (Tokatlidis *et al.*, 2006). Given that Y_{max} values were not higher than the respective Y_{obt} values, family H10 is expected to have the highest crop yield potential. On the basis of the parabolic response curves there is also a sign of family's L8 superiority over families H4, H8 and cv. *Nestos*.

Results of the two models are given in Table 1. Crop yield potential is distinguished by the first model into expected yield potential per plant (α) and tolerance to increasing plant density at the single-plant level (b^{-1}) that end up to the expected crop yield potential (Y_{pot}). By the second model relative crop yield potential (Y_{ci}) is approached through yield potential per plant ($\overline{X}$), tolerance to overall stresses ($\overline{X}\sigma_p^{-1}$) and responsiveness to inputs $\{(\overline{X}_s-\overline{X})\sigma_p^{-1}\}$.

$Y(t\ ha^{-1})$	1	2	3	PR 3183	B73xMo17
Y_{obt}	10.02	10.25	9.79	10.45	10.53
Y_{max}	10.07	10.27	9.82	10.53	12.16

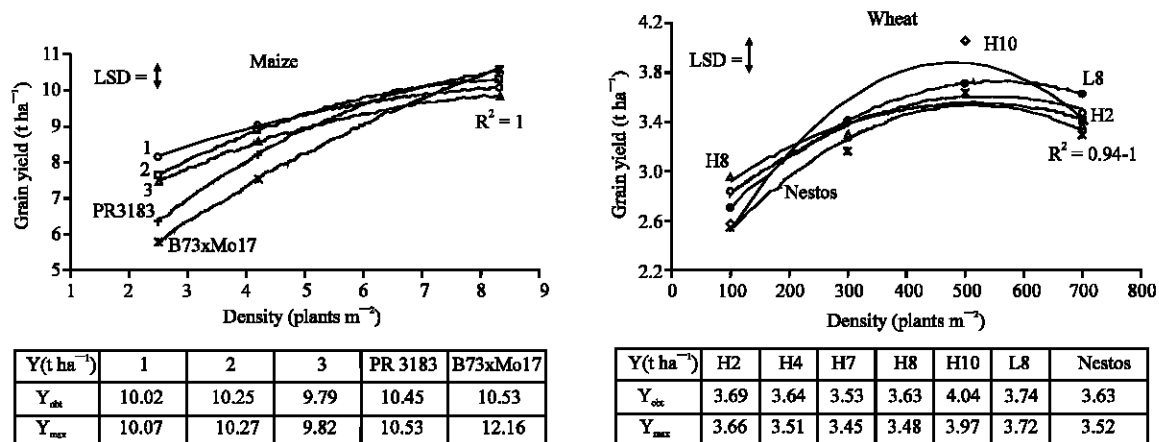| $Y(t\ ha^{-1})$	H2	H4	H7	H8	H10	L8	Nestos
Y_{obt}	3.69	3.64	3.53	3.63	4.04	3.74	3.63
Y_{max}	3.66	3.51	3.45	3.48	3.97	3.72	3.52

Fig. 1: Curvilinear grain yield response to density changes at the unit area level of maize and wheat genotypes. Grain yield obtained (Y_{obt}) at the density approximating those commercially used (8.3 and 500 plants m^{-2} for maize and wheat, respectively) and maximum grain yield (Y_{max}) derived from the parabolic response curve of grain yield versus density, are also given. Strong genotype by density is revealed questioning the reliability of crop yield potential estimation under a single density, whereas maize entry 1 and wheat entry H2, characterized by improved yield potential per plant, appear less density dependent than the respective check entries B73xMo17 and cv *Nestos*

Table 1: Crop yield potential estimated by two models. First model (A): Results from linear regression analysis of yield per plant in grams (Y_p) on plant density in plants/m^2 (D), expressed by the equation $Y_p = \alpha - bD$ and based on data obtained at three densities for maize and four densities for wheat: Expected yield potential per plant in grams (α), tolerance to increasing plant density (b^{-1}) and expected crop yield potential in t ha^{-1} (Y_{pot}) calculated by the formula $Y_{pot} = (1/4)\ \alpha^2 b^{-1}$. Second model (B): The three crop yield components derived from data obtained at the ultra-low density of 0.74 plants m^{-2} for maize and 1.2 plants/m^2 for wheat: Yield potential per plant in grams ($\overline{X}$), tolerance to stresses ($\overline{X}\sigma_p^{-1}$) and responsiveness to inputs $\{(\overline{X}_s - \overline{X})\sigma_p^{-1}\}$. Each component value divided by the respective value of check (B73xMo17 for maize, *Nestos* for wheat) constituted the component index (values in parenthesis). The sum of the three indexes for each entry resulted in its crop yield potential combined index (Y_{ci})

	A. First model			B. Second model			
Entry	α	b^{-1}	Y_{pot}	$\overline{X}$	$\overline{X}\sigma_p^{-1}$	$(\overline{X}_s - \overline{X})\sigma_p^{-1}$	Y_{ci}
Maize							
1	384.1	0.03	11.26	1438 (3.20)	5.26 (2.00)	7.34 (3.62)	8.81
2	359.6	0.03	11.05	1396 (3.10)	5.00 (1.90)	7.20 (3.55)	8.55
3	351.8	0.03	10.67	1275 (2.83)	4.35 (1.65)	6.85 (3.37)	7.86
PR 3183	296.3	0.05	10.48	668 (1.48)	4.55 (1.73)	10.85 (5.34)	8.56
B73xMo17	263.8	0.06	10.26	450 (1.00)	2.63 (1.00)	2.03 (1.00)	3.00
Wheat							
H2	2.767	270	5.171	31.09 (1.25)	1.92 (1.21)	2.56 (1.12)	3.59
H4	2.824	263	5.246	34.15 (1.38)	1.62 (1.02)	2.72 (1.19)	3.60
H7	2.681	278	4.993	33.47 (1.35)	2.03 (1.28)	2.07 (0.91)	3.54
H8	2.868	256	5.274	32.18 (1.30)	1.90 (1.20)	2.48 (1.08)	3.59
H10	2.576	303	5.025	31.22 (1.26)	1.60 (1.01)	2.43 (1.06)	3.33
L8	2.665	286	5.072	29.19 (1.18)	1.70 (1.08)	2.53 (1.11)	3.36
Nestos	2.515	303	4.792	24.75 (1.00)	1.58 (1.00)	2.28 (1.00)	3.00

On the basis of the first model recycled maize hybrids 1, 2 and 3 appear to have improved α values compared to either their original hybrid PR 3183 or the check hybrid B73xMo17. According to this model their yield potential per plant was higher by 19 to 30% compared to PR 3183 and by 33 to 46% compared to B73xMo17. Considering tolerance to density at the single-plant level hybrids PR 3183 and B73xMo17 had by 67 and 100%, respectively, higher b^{-1} values in comparison with the recycled hybrids. The recycled hybrid 1 had the highest

Y_{pot} value (7.4% over PR 3183 and 9.7% over B73xMo17), whereas the recycled hybrids 2 and 3 exceeded hybrid PR 3183 by 5.4 and 1.8%, respectively and hybrid B73xMo17 by 7.7 and 4%, respectively. According the second model, yield potential per plant of the three recycled hybrids, determined directly at the single ultra-low density of 0.74 plants m^{-2}, was up to 115% higher than yield potential per plant of the original hybrid PR 3183. Standardized entry means ($\overline{X}\sigma_p^{-1}$) reflect stronger tolerance to overall stresses of the recycled

hybrids 1 and 2, compared to hybrids PR 3183 and B73xMo17. As far as capacity to exploit favourable environmental resources is concerned, $(\overline{X}_s\text{-}\overline{X})\sigma_p^{-1}$ values showed that, the recycled hybrids were superior over the check hybrid B73xMo17, but inferior to their original hybrid PR 3183. Incorporation of the three components into a single combined index (Y_{ci}) resulted in values showing that recycled hybrids, as well as hybrid PR 3183, were superior over the check hybrid B73xMo17. Among the three recycled hybrids the highest Y_{ci} value was found for hybrid 1 and the lowest for hybrid 3, whereas hybrid 2 was equivalent to the original hybrid PR 3183.

The expected yield potential per plant (α) of the six wheat families derived from cv *Nestos* was by 2.4 (H10) till 14% (H8) higher in comparison with α value of the original cultivar. In regards with tolerance to density at the single-plant level (b^{-1}), likewise in maize hybrids, higher α values were associated with lower b^{-1} values, since family H10 with the lowest α value among the six families had the same b^{-1} value with original cv. *Nestos*, while family with the highest α value (H8) had the lowest b^{-1} value (15.5% lower than that of H10 and cv *Nestos*). Derived families had Y_{pot} values by 5 to 10% higher than that of cv *Nestos* and among them family H10 was by 2.8, 4.2 and 4.7% inferior in comparison with families H2, H4 and H8, respectively. Family L8 had by 2, 3.3 and 3.8% lower Y_{pot} values than families H2, H4 and H8, respectively. Derived families exceeded cv *Nestos* for the three components of the second model, family H7 excepted in case of the third component. Among the five families with significant superiority over their original cultivar for mean yield per plant (Tokatlidis *et al.*, 2006), family H10 had the lowest and family H4 the highest $\overline{X}$ value (26 and 38% over cv *Nestos*). Standardized entry means showed that families H2, H7 and H8 seemed to be more tolerant to overall stresses, in comparison with family H10 and cv *Nestos*. Moreover, families H2 and H8 (as well as H4 and L8) exhibited of the highest $(\overline{X}_s\text{-}\overline{X})\sigma_p^{-1}$ values. Consequently, families H2 and H8 were those that combined the highest values for all the three components. Families H2, H4 and H8 were equivalent in regards with their combined indexes (Y_{ci}), which were by about 7, 8 and 20% larger than those of families L8, H10 and cv. *Nestos*, respectively. Thus the second model alike to the first one, suggests that families H2, H4 and H8 are expected to have the highest crop yield potential.

The following interferences could be drawn in regards with crop yield potential approximation by the two models. The two models consider a common component of crop yield potential, the yield potential per plant, as it expressed under conditions simulating the absence of any kind of stresses (i.e., when density is so low that there is no interplant interference of competition within the crop stand, whereas measures are taken to control weeds, diseases, insects and to ensure adequate water and nutrient resources). Yield potential per plant, however, is approached indirectly by the first model (α values) and directly by the second one ($\overline{X}$ values). Comparison between theoretically expected (α) with experimentally obtained ($\overline{X}$) yield potential per plant, evidences that the first model underestimated the capacity of tested genotypes to yield at the single-plant level (e.g., 384 vs 1438 g of maize hybrid 1 and 2.77 vs 31.09 g of wheat family H2). Nevertheless, the two models estimated this particular component in a similar way, bolstered by the high simple correlation coefficients between α and $\overline{X}$ values (r = +0.99, p<0.004 in case of maize and r = +0.72, p<0.08 in case of wheat) indicating that α value constitutes a comparatively good estimate of yield potential per plant. Both models strongly emphasize this particular component of crop yield potential, since it is the determinant parameter to compute Y_{pot} values in the first model and constitute the key measurement of the second and third component in the second model. It is noteworthy to mention that Duvick (1997) reported unchanged so far yield potential per plant in case of maize hybrids and suggested future improvements in this trait under low stress environments. Yan and Wallace (1995) pointed out: Although all plant breeders realize that modern cultivars are more suitable for high-density cultivation because of improved lodging resistance, few breeders have paid attention to the contribution toward high yield through improvement in the yield potential per plant. Consequently, yield per plant in the absence of competition deserves particular consideration to test a genotype's background for advanced crop yield potential. Both recycled maize hybrids and wheat families were found to exhibit improved yield potential per plant than their original material, estimated either indirectly (α-values), or directly ($\overline{X}$-values). This was the result of the method applied to derive them (Tokatlidis *et al.*, 1998; 2006), which was selection on the basis of single-plant yield and under conditions allowing yield potential per plant to be fully expressed (i.e., ultra-low densities simulating absence of competition). Low-stress conditions maximize phenotypic expression and differentiation (Fasoula and Fasoula, 2002), accentuating thus existing or newly developed genetic variation even within a genetically narrow pool like a wheat cultivar (Tokatlidis *et al.*, 2006). In Fig. 2 the linear response of maize genotypes to density changes at the single-plant level is given, as the first model demands. It is evident that differentiation of entries increase as density
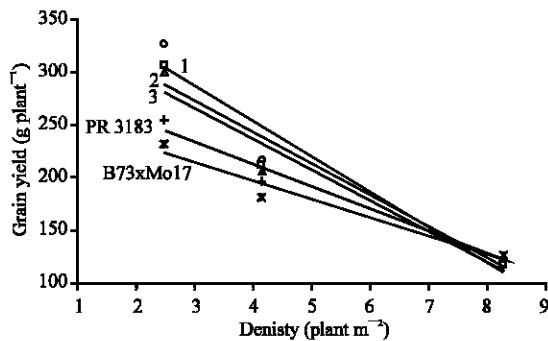
Fig. 2: Grain yield response of the maize hybrids (recycled 1, 2, 3, their original PR 3183 and B73xMo17) to density changes at the single-plant level (linear, R^2 = 0.92-0.97). Lower densities enhance entries' differentiation, leading entries with improved yield potential per plant to respond more drastically to density changes and according to the first model to be assumed more sensitive to density stress, an impact revealing a strong negative relationship between the two crop yield potential components of the first model

decreases, reaching maximum level at the ultra-low density that excludes any plant-to-plant interference for environmental resources. The impact also explains why α values were too low in comparison with $\overline{X}$-values (Table 1), especially in case of wheat entries due to higher gap between the lowest density used to approach α and the ultra-low density assumed to represent absence of competition (i.e., 100 vs 1.2 plants m^{-2}). Actually, α-values strongly depend on the lowest density used to estimate them and the more the lowest density approximates real absence of competition the higher α values are expected. For wheat genotypes, if linear regression analysis is conducted excluding the lowest density of 100 plants m^{-2}, α values are by around 45% lower in comparison with those of Table 1, whereas in case of maize hybrids when the lowest density of 2.5 plants m^{-2} is excluded, α values are by 10% lower for hybrid PR 3183 and by 17-20% lower for hybrids 1, 2, 3 and B73xMo17.

Considering tolerance to increasing plant density, controversial inferences are drawn when b^{-1} values are compared with $\overline{X}\sigma_p^{-1}$ values (Table 1). Hybrids PR 3183 and B73xMo17 had by 67 and 100%, respectively, higher b^{-1} values in comparison with the recycled hybrids. In turn, the three recycled hybrids, characterized by improved yield potential per plant, seem to be more sensitive to density changes at the single-plant level, as it is apparent from Fig. 2 where lines of recycled hybrids

decline more sharply than those of PR 3183 and B73xMo17. Consequently, high α values were associated with low b^{-1} values. The same impact is apparent in case of wheat, when genotypes with the lowest α values (family H10 and cv *Nestos*) are compared with those having the highest α values (families H2, H4 and H8). Data showed a strong negative relationship between α and b^{-1} values and simple correlation coefficients were high and significant (r = -0.97, p<0.007 and -0.98, p<0.001 in maize and wheat, respectively). The impact is reasonable, because of the negative association between phenotypic expression and differentiation with plant density. This means that differences between entries increase as density decrease, so linear response of yield to density changes is mounting in case of improved yield potential per plant. Obviously, intercept b of equation Y_p = α-bD will be highest for entries with highest yields per plant at low densities. The conclusion is that b^{-1} values as a measure of density tolerance have a sense only among genotypes equivalent for yield potential per plant, otherwise undervalue the superior ones, as it is evidenced when either recycled hybrids are compared with hybrids PR 3183 and B73xMo17, or families H2, H4 and H8 are compared with family H10 and cv *Nestos*. On the contrary, in the hypothetical case of equivalent entries at high densities, it is also obvious that those with higher yields at lower densities would be more desirable, although their b^{-1} values will be lower. Negative relationship between α and b^{-1} values (r = -0.96, p<0.001) is also drawn from results obtained when Yan and Wallace (1995) reanalyzed data from Tollenaar (1989) regarding nine older and newer maize hybrids. That led Yan and Wallace (1995) to state that the increased crop yield of newer hybrids was achieved through the improvement of yield potential per plant, accompanied by a reduced tolerance to crop density. However, other reports claimed totally opposite statements. Duvick (1997) evaluated 36 hybrids released from 1934 to 1991 and found that at the very low density of 1 plant/m^2 there was no increase in grain yield over time, showing that breeding failed to improve yield potential per plant. Duvick and Cassman (1999) speculated: on the basis of a definition of yield potential as the yield that can be achieved with an adapted hybrid when grown without obvious stress of any kind, we found that there is conflicting evidence to support that maize yield potential has improved. Sangoi *et al.* (2002) evaluated three maize hybrids representing three different eras and found the newer hybrid to be superior over the two older hybrids at the highest density, but by around 10% inferior at the lower density. Data from Duvick (1997) demonstrated that

the superiority of newer hybrids was partly attributed to their ability to tolerate and thus to exploit higher densities. It has been known for several decades that newer maize hybrids are more tolerant to high plant population density (Tollenaar and Lee, 2002). Conclusively, these findings question the reliability of b^{-1} values to comparatively assess tolerance to density of genotypes that differ in their ability to yield at the single-plant level. In fact b^{-1} values have been reported as measure of optimum for maximum crop yield density (Tollenaar, 1989, 1992) and found to be negatively associated with yield potential per plant (Tokatlidis, 2001). On the other hand, tolerance to stresses suggested by the second model, is referred to any kind of stresses at the crop stand level, including thus tolerance to increased plant densities (Fasoula and Fasoula, 2002). In contrast to the strong negative association between α and b^{-1} values, $\overline{X}$ vs $\overline{X}\sigma_p^{-1}$ values (Table 1) show that improved yield potential per plant is not necessarily accompanied by reduced tolerance to stresses. The recycled hybrids, found by the first model sensitive to density changes, are seemed to be more tolerant than hybrid B73xMo17. The same is observed from Table 1, regarding families H2 and H8 in relevance with family H10 and cv *Nestos*.

Figure 1 shows that the recycled maize hybrids appear to be less density dependent when compared with hybrids PR 3183 and B73xMo17 and the same is obvious for wheat families H2 and H8, as well as H4 (not shown), in comparison with family H10 and cv *Nestos*. The impact has been thoroughly discussed in previous studies (Tokatlidis, 2001, 2006). Briefly, genotypes that combine improved yield potential per plant and tolerance to stresses have the capacity to achieve maximum crop yield at comparatively wider range of densities, because the first parameter extends the lower limit of the optimum density and the second one extends the upper limit of the optimum density, rendering thus genotypes density-independent (Fasoula and Fasoula, 2002). Density-independent cultivars are more dependable because they have the advantage to adequately compensate any yield loss due to commonly occurred situation of missing plants in the field. Nafziger (1996) speculated that missing plants in maize fields are inevitable, where 5 to 15% of dropped seeds normally fail to produce plants. Tokatlidis and Koutroubas (2004) highlighted the necessity for density-independent maize hybrids development, while Fasoula and Fasoula (2002) and Tokatlidis *et al.* (2005) referred to benefits from using such cultivars. Duvick (2005) commented: Theoretically it may be possible to raise yields per unit area by increasing yield per plant while holding population constant (at lower densities

than present norms) and such a goal might be practical for hybrids suited for drought-prone environments, where planting at lower density is prudent but the ability to utilize occasional higher rainfall by increasing yield per plant would be desirable. Even though graphs of Fig. 1 suggest that hybrids PR 3183 and B73xMo17, as well as families H10 and L8, are potent to give the highest crop yield among the maize and wheat genotypes, respectively, Y_{pot} and Y_{ci} values (Table 1) give a totally different impression. Estimated by Y_{pot} crop yield potential appears higher for recycled hybrids, despite their sensitiveness to density according to the first model, thanks to their improved yield potential per plant. Regarding Y_{ci} values, the recycled hybrids were found superior over hybrid B73xMo17. Compared to their original hybrid PR 3183, recycled hybrids 1 and 2 had higher and equivalent Y_{ci} values, respectively, although on the basis of the third component (i.e., responsiveness to inputs) they seem to be less capable to exploit favourable environmental resources. Regarding the wheat genotypes and compared with family H10, families H2, H4 and H8, although found more sensitive to density at the single-plant level, had by 2.9, 4.4 and 5% higher Y_{pot} values, respectively, as a result of higher α values. They had also by 2-4% higher Y_{pot} values than family L8. These three entries gave the highest Y_{ci} values, being by 6.8 and 7.8% higher compared to families L8 and H10. Consequently, both models support families H2, H4 and H8 of having the most advanced crop yield potential among the wheat entries.

The first model approaches crop yield potential through α, b^{-1} and Y_{pot}, values of which depend on the lowest level of density used. Analysis of data presented by Tollenaar (1992) regarding two double-cross and two single-cross hybrids grown at a range of eight densities (0.5, 1, 2, 4, 8, 12, 18, 24 plants m^{-2}) are indicative. Linear regression analysis of yield per plant on plant density using data including as lowest density that of 4 plants m^{-2} and progressively those of 2, 1 and 0.5 plants m^{-2}, results to the following respective values for one of the tested hybrids (e.g., single-cross PR 3902): α: 169, 215, 256 and 282 g plant^{-1}, b^{-1}: 0.15, 0.11, 0.09 and 0.08 and Y_{pot}: 10.76, 12.53, 14.09 and 15.08 t ha^{-1}. The same impact is found for the rest three hybrids. Obviously, as the lowest density decreases, α increases and b^{-1} decreases, but since equation for Y_{pot} considers the square of α, Y_{pot} values also increase. Despite this differentiation, hybrids' rank for any of these three parameters does not change. Therefore, although Y_{pot} values are expressed in real units of yield per unit area, they have relative value and as happens with Y_{ci} values of

the second model, can be used only comparatively for the entries being tested in a particular study. Data of the study showed a relatively good fit between the two models of crop yield potential approximation, since both suggested the same genotype of being potent to give the highest crop yields (i.e., recycled hybrid 1 among maize genotypes and families H2, H4, H8 among wheat genotypes). Positive simple correlation coefficients (r) between Y_{pot} and Y_{ci} values were found, which were for maize material + 0.71 (not significant due to limited data) and +0.88 (p<0.03) for wheat material. Undoubtedly, these preliminary data could not be assumed unequivocal. However, the two models are supportive of yield potential per plant being a significant piece of crop yield potential puzzle and constituting a parameter that should be taken into account by breeders and agronomists. Hybrids with improved yield potential per plant have been documented to exhibit small yield decreases at low densities (Sarquis *et al.*, 1998; Tokatlidis *et al.*, 2001). The first model, although undervalues tolerance to stresses of genotypes characterised by improved yield potential per plant, ended up to favour them as being the most promising for higher crop yield potential. Their advantage, that renders them more desirable, is the capacity to give maximum grain yield per unit area under wider range of plant densities, the primarily pursued target of the second model. In other words both models favour density-independent cultivars. However, the second model seems to have a number of advantages over the first one. There is no the demand of at least two densities and a single ultra-low density is enough, simplifying experimentation. Key component of crop yield potential (i.e., yield potential per plant), which essentially constitutes the evaluation unit in both models, is measured in a more direct and accurate way. It seems to consider crop yield potential in a more integrated manner involving tolerance to overall stresses and responsiveness to inputs. Crop yield potential components could be used as both evaluation and selection criteria, so promising genotypes could be distinguishable from the first generations. On the other hand, the demand for at least two densities renders application of the first model for a large number of genotypes almost impossible. In case prospective studies prove that crop yield potential assessment at the ultra-low density that allows full expression of yield potential per plant is reliable, the second model, given that simplifies experimentation, brings a revolutionary change in the crop breeding procedures to satisfy the demand for productive, adaptable and dependable cultivars. In a recent work Papadopoulos *et al.* (2007) successfully predicted crop yield potential in dry bean (*Phaseolus vulgaris* L.)

genotypes by the second model. According to Fasoula and Fasoula (2002), the second model represents an integral part of a whole breeding approach rather than an isolated theoretical concept and its capacity to successfully select with efficiency and accuracy in every generation of selection for productivity, stability and adaptability has been validated with experimental reports (Traka-Mavrona *et al.*, 2000; Ntanos and Roupakias, 2001; Tokatlidis *et al.*, 2006; Fasoula and Boerma, 2007; Papadopoulos *et al.*, 2007). The second model also leads to the creation of density-independent cultivars, i.e., to cultivars that attain optimal crop yield over a wide range of crop densities (Fasoula and Fasoula, 2002; Tokatlidis, 2001; Tokatlidis *et al.*, 2006), reflecting additional advantages: (1) The density-independent cultivars may exploit the benefits of medium plant densities, e.g., drought resistance, reduced lodging, etc. (Fasoula and Fasoula, 2002; Tokatlidis and Koutroubas, 2004; Tokatlidis *et al.*, 2005). (2) In case of no ideal germination, re-sowing is not necessary. (3) It is the product of joint selection for high and stable crop yield at ultra-low densities that erase the confounding effects of competition, thereby increasing selection efficiency (Fasoula and Fasoula, 1997; Janick, 1999). (4) In comparisons among cultivars the confounding effect of genotype by density interaction is absent. (5) It excludes density per se being a component of the crop yield potential, as demanded by the first model.

CONCLUSIONS

Results of the study could be summarized as follows. To comparatively estimate crop yield potential one could not count upon data from density assumed as optimum to give the highest yield per unit area, due to genotype by density interaction. Both models consider the single-plant yield as evaluation unit instead of the yield per unit area. Yield potential per plant, defined as the ability of a genotype to yield at the single-plant level in the absence of competition, constitutes the first and the determinant component of crop yield potential. However, the second model determines yield potential per plant in a more direct and accurate way. The two models suggest that this parameter deserves particular consideration to estimate a genotype's background for high crop yield potential. For this reason, genotypes that seem to be less dependent on plant density to achieve maximum yield per unit area are supported as the most promising for high crop yield potential. The first model also considers tolerance to density as component of crop yield potential, but comparative evaluation for tolerance to density seems to

undervalue genotypes with improved yield potential per plant and hence, reveals a strong negative relationship between the two components. Foregoing discussion evidences that the way the first model approximates tolerance to density is questionable. In addition to yield potential per plant, the second model considers tolerance to any kind of stresses, as well as ability to respond to inputs, considering crop yield potential in a more integrated manner.

REFERENCES

Batzios, D.P. and D.G. Roupakias, 1997. Honey: A microcomputer program for plant selection and analyses of the honeycomb designs. Crop Sci., 37 (3): 744-747.

Berzsenyi, Z. and Q.L. Dang, 2006. Effect of crop production factors on the yield and yield stability of maize (*Zea mays* L.) hybrids. Acta Agron. Hung., 54 (4): 413-424.

Clarke, F.R., R.J. Baker and R.M. DePauw, 1998. Interplot interference distorts yield estimates in spring wheat. Crop Sci., 38 (1): 62-66.

Duvick, D.N., 1997. What is yield? In: Edmeades, G.O. *et al.* (Ed.). Developing Drought and Low N-tolerant Maize. CIMMYT, El Batan, Mexico, pp: 332-335.

Duvick, D.N. and K.G. Cassman, 1999. Post-green revolution trends in yield potential of temperate maize in the North-Central United States. Crop Sci., 39 (6): 1622-1630.

Duvick, D.N., 2005. The contribution of breeding to yield advances in maize (*Zea mays* L.). Adv. Agron., 86: 83-145.

Evans, L.T. and R.A. Fischer, 1999. Yield potential: Its definition, measurement and significance. Crop Sci., 39 (6): 1544-1551.

Fasoula, D.A. and V.A. Fasoula, 1997. Competitive ability and plant breeding. Plant Breed. Rev., 14: 89-138.

Fasoula, V.A. and D.A. Fasoula, 2002. Principles underlying genetic improvement for high and stable crop yield potential. Field Crops Res., 75 (2-3): 191-209.

Fasoula, V.A. and H.R. Boerma, 2007. Intra-cultivar variation for seed weight and agronomic traits. Crop Sci., 47 (1): 367-373.

Fasoulas, A.C. and V.A. Fasoula, 1995. Honeycomb selection designs. Plant Breed. Rev., 13: 87-139.

Janick, J., 1999. Exploitation of heterosis: Uniformity and stability. In The Genetics and Exploitation of Heterosis in Crops, 319-333 (Ed ASA-CSSA-SSSA), Madison, WI. USA.

Lloveras, J., J. Manent, J. Viudas, A. Lúpez and P. Santiveri, 2004. Seeding rate influence on yield and yield components of irrigated winter wheat in a Mediterranean climate. Agron. J., 96 (5): 1258-1265.

Nafziger, E.D., 1996. Effects of missing and two-plant hills on corn grain yield. J. Prod. Agric., 9 (2): 238-240.

Ntanos, D.A. and D.G. Roupakias, 2001. Comparative efficiency of two breeding methods for yield and quality in rice. Crop Sci., 41 (2): 345-350.

Papadopoulos, I.I., I.S. Tokatlidis, E.G, Tamoutsidis, M. Koutsika-Sotiriou and S. Koutroubas, 2007. Crop yield potential estimation under too low density in dry bean genotypes. Int. J. Plant Breed. Genet., 1 (2): 75-81.

Sangoi, L., M.A. Gracietti, C. Rampazzo and P. Bianchetti, 2002. Response of Brazilian maize hybrids from different eras to changes in plant population. Field Crops Res., 79 (1): 39-51.

Sarlangue, T., F.H. Andrade, P.A. Calvino and L.C. Purcell, 2007. Why do maize hybrids respond differently to variations in plant density? Agron. J., 99 (4): 984-991.

Sarquis, J.I., H. Gonzalez and J.R. Dunlap, 1998. Yield response of two cycles of selection from a semiprolific early maize population to plant, sucrose infusion and pollination control. Field Crops Res., 55 (1-2): 109-116.

Tokatlidis, I.S., M. Koutsika-Sotiriou, A.C. Fasoulas and A.S. Tsaftaris, 1998. Improving maize hybrids for potential yield per plant. Maydica, 43 (2): 123-129.

Tokatlidis, I.S., 2000. Variation within maize lines and hybrids in the absence of competition and relation between hybrid potential yield per plant with line traits. J. Agric. Sci., 134 (4): 391-398.

Tokatlidis, I.S., 2001. The effect of improved potential yield per plant on crop yield potential and optimum plant population in maize hybrids. J. Agric. Sci., 137 (3): 299-305.

Tokatlidis, I.S., M. Koutsika-Sotiriou and A.C. Fasoulas, 2001. The development of density-independent hybrids in maize. Maydica, 46 (1): 21-25.

Tokatlidis, I.S. and S.D. Koutroubas, 2004. A review study of the maize hybrids' dependence on high plant populations and its implications on crop yield stability. Field Crops Res., 88 (2-3): 103-114.

Tokatlidis, I.S., M. Koutsika-Sotiriou and E. Tamoutsidis, 2005. Benefits from using maize density-independent hybrids. Maydica, 50 (1): 9-17.

Tokatlidis, I.S., I.N. Xynias, J.T. Tsialtas and I.I. Papadopoulos, 2006. Single-plant selection at ultra low density to improve stability of a bread wheat cultivar. Crop Sci., 46 (1): 90-97.

Tollenaar, M., 1989. Genetic improvement in grain yield of commercial maize hybrids grown in Ontario from 1959 to 1988. Crop Sci., 29 (6): 1365-1371.

Tollenaar, M., 1992. Is low plant density a stress in maize? Maydica, 37 (4): 305-311.

Tollenaar, M. and J. Wu, 1999. Yield improvement in temperate maize is attributable to greater stress tolerance. Crop Sci., 39 (6): 1597-1604.

Tollenaar, M. and E.A. Lee, 2002. Yield potential, yield stability and stress tolerance in maize. Field Crops Res., 75 (2-3): 161-169.

Traka-Mavrona, E., D. Georgakis, M. Koutsika-Sotiriou and T. Pritsa, 2000. An integrated approach of breeding and maintaining an elite cultivar of snap bean. Agron. J., 92 (5): 1020-1026.

Yan, W. and D.H. Wallace, 1995. Breeding for negatively associated traits. Plant Breed Rev., 13: 141-177.