

Improved Plant Yield Efficiency is Essential for Maize Rainfed Production

Ioannis S. Tokatlidis,* Christos Dordas, Fokion Papathanasiou, Ioannis Papadopoulos, Chrysanthi Pankou, Fotakis Gekas, Elissavet Ninou, Ioannis Mylonas, Constantinos Tzantarmas, Jovanka-Katarzyna Petrevska, Anastasia Kargiotidou, Iosif Sistanis, and Anastasios Lithourgidis

ABSTRACT

Plant yield efficiency reflects the single-plant yield at low density that precludes interplant interference for resources. The role of plant yield efficiency in adaptation to water deficit was investigated in maize (*Zea mays* L.). Also investigated was whether yield of space-planted environments is transferable to densely seeded situations. Further, the correlation and genotype by environment ($G \times E$) interaction of spaced and densely seeded plots were investigated. Thirty-one lines and 31 crosses among them were tested in three locations under dense stand and the ultra low density of 0.74 plants m^{-2} as well as in normal and deficit irrigation treatments. The dense stand was 4.44 plants m^{-2} in the water deficit regime and 6.67 plants m^{-2} (lines) and 7.84 plants m^{-2} (hybrids) in the normal water treatment. Hybrids of greater plant yield efficiency were less sensitive to water shortage. Among four hybrids yielding the same at normally irrigated dense stand (11.50 Mg ha^{-1}), yield loss due to water shortage was 46% for that of the lowest plant yield efficiency (645 g $plant^{-1}$) and 17% for that of the highest plant yield efficiency (880 g $plant^{-1}$). Correlations between hybrid plant yield efficiency and gas exchange water-use efficiency in dense stand were significant. The low density ensured $G \times E$ interaction in the quantitative aspect only and thus was of higher heritability, placing emphasis on parental yield per se. Plant yield efficiency is a key element of hybrid ability to withstand water shortage and cope with environmental heterogeneity.

Ability of a cultivar to tolerate crowding but also perform well at the single-plant level has been asserted to be a determinant element to its crop yield potential (Yan and Wallace, 1995; Fasoula and Tokatlidis, 2012). However, in maize yield more improvement has resulted from improving tolerance to high plant population densities rather than single-plant performance; the per plant yield under minimal competition for light, water, and nutrients remained unchanged (Tollenaar and Lee, 2002; Duvick, 2005). Transition to higher populations in combination with stagnation in yield capacity of individual plants resulted in hybrids characterized as density-dependent (Fasoula and Tollenaar, 2005; Tokatlidis et al., 2011). Individual hybrids respond differently to plant density (Cox, 1996; Sangoi et al., 2002), periodic reassessment of optimum hybrid

plant density is necessary (Widdicombe and Thelen, 2002; Cox and Cherney, 2012), and profit-maximizing density might not coincide with yield-maximizing density (Popp et al., 2006). Density dependence is associated with interseasonal variation in optimum density followed by instability and yield loss, particularly for rainfed maize under the diverse agro-ecosystems induced by ongoing climate change (Duvick, 2005; Berzsenyi and Tokatlidis, 2012; Tokatlidis, 2013, 2014).

Regarding the aforementioned analysis, two implicit assumptions arise. First, agronomists and breeders should consider individual plant performance (Yan and Wallace, 1995; Duvick, 2005; Fasoula and Tollenaar, 2005; Tokatlidis et al., 2011). Plant yield efficiency (PYE), reflecting the ability of individual plants to efficiently capture resources, is measurable only at very low densities that eliminate interplant competition (Fasoulas, 1993; Fasoula and Tokatlidis, 2012). Since the primary selection goal is always high yield potential on a per-area basis, the correlation between spaced plants vs. performance of the same genotype in a densely seeded situation would allow selection in space-planted nurseries (Hansen et al., 2005). Second, evaluation of different maize genotypes at a single stand presumably appears biased, as it was analyzed by Tokatlidis (2013). Instead, absence of interplant competition devoid of confounding yield by density interactions allows for more comparable evaluation of different genotypes (Fasoulas, 1993; Fasoula and Fasoula, 2000; Fasoula and

Supplemental material available online. I.S. Tokatlidis, C. Tzantarmas, and A. Kargiotidou, Dep. of Agricultural Development, Democritus Univ. of Thrace, Orestiada, 68200, Greece; C. Dordas, C. Pankou, F. Gekas, E. Ninou, I. Mylonas, and A. Lithourgidis, School of Agriculture, Aristotle Univ. of Thessaloniki, Thessaloniki, 54124, Greece; F. Papathanasiou, I. Papadopoulos, J.K. Petrevska, and I. Sistanis, Dep. of Agricultural Technology, Technological Educational Institute of Western Macedonia, Florina, 53100, Greece. Received 22 Nov. 2014. Accepted 1 Feb. 2015. *Corresponding author (itokatl@agro.duth.gr; itokatl@hotmail.com).

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Abbreviations: A, assimilation rate; ASI, anthesis-silking interval; $G \times E$, genotype by environment interaction; HI, harvest index; PYE, plant yield efficiency; T, transpiration; WUE, water-use efficiency.

Tokatlidis, 2012). Hence, the correlation between widely spaced plants and common farming densities is a reasonable challenge.

The assessment of different genotypes for yield capacity is also faced with $G \times E$ interaction, which is unavoidable in field experiments (Sabaghnia et al., 2010). The differential genotypic expression across environments reduces the association between phenotypic and genotypic values, causing selections from one environment to perform poorly in another (Romagosa and Fox, 1993). Whether the $G \times E$ interaction is a matter of scale without changing the rank of genotypes from one environment to another (non-crossover) is considered quantitative. Quantitative interaction is less important to breeders than the qualitative or crossover interaction, in which genotype rank changes and complicates selection and identification of superior genotypes (Baker, 1988).

Biomass production is tightly linked to increased photosynthetic rate and transpiration. Breeding for maximal water capture and use for increased transpiration are important targets for yield improvement under unfavorable water conditions (Tambussi et al., 2007; Tardieu et al., 2014). Gas exchange water-use efficiency (WUE), defined as the net CO_2 assimilated by photosynthesis (A) divided by the water transpired in the same time period (T), is related to the genotypic capacity to use available water and, therefore, sustain transpiration under water shortage conditions (Lopes et al., 2011). Responses of agronomic traits, such as delay in silk growth (anthesis-silking interval; ASI) and lower harvest index (HI), are typical reactions of maize under drought stress (Bolanos and Edmeades, 1996). Reduced ASI recurrently has been selected among other traits aiming to improve partitioning of assimilates to the ear, increasing yield performance (Duvick, 2005; Lopes et al., 2011). Similarly, increased HI through a better exploitation and better ability to devote more assimilates to the grain might indicate genotype tolerance to drought (Monneveux et al., 2006; Carena et al., 2009).

The necessity to prioritize PYE, qualified as an essential prerequisite for effective use of resources under varying conditions (Tokatlidis et al., 2011; Tokatlidis, 2013, 2014), brings to the forefront space-planted nurseries. The main objectives of this study included the following: (i) investigate the role of hybrid PYE in terms of yield performance and adaptation to water-deficit conditions and find possible connections of PYE with WUE, ASI, and HI; (ii) determine the correlations of yield performance of widely spaced and densely seeded plots while also investigating the respective $G \times E$ interactions. Results could provide information on whether yield of space-planted environments can be transferred to densely seeded situations.

MATERIALS AND METHODS

A set of 25 inbred lines provided by American Genetics Inc. and a set of six experimental lines were tested during the 2012 growing season (Supplemental Table S1). According to the owner company, the first set was of commercial interest including parents of cultivated hybrids (corresponding codes in the study were 1c–24c and 31c). The set of experimental lines (coded 25e–30e) had been derived through selection in the absence of competition on single-plant yield (Tokatlidis et al., 1998), placing particular emphasis on plant yield efficiency. The line coded 23 was omitted from final analysis due to poor emergence. Thirty-one hybrids, obtained from single crosses among the aforementioned lines, were tested during the 2013

season. Twenty crosses were chosen so as to include one parent from each set, while both parents of 7 and 4 out of the 31 crosses were from the commercial and the experimental set, respectively (Supplemental Table S2). Field experiments were established in three locations in northern Greece, henceforth named Site1, Site2, and Site3. Site1 was the farm of the Aristotle University of Thessaloniki (40°32' N, 22°59' E, 0 m asl), on a sandy loam soil with pH 7.8, organic matter 11.5 g kg⁻¹, N-NO₃ 65.0 mg kg⁻¹, P-Olsen 15.3 mg kg⁻¹, K 313 mg kg⁻¹, and water holding capacity 25.3%. Site2 was the farm of the Technological Education Institute of Western Macedonia in Florina (40°46' N, 21°22' E, 707 m asl), on a sandy loam soil with pH 6.3, organic matter 14.0 g kg⁻¹, N-NO₃ 100 mg kg⁻¹, P-Olsen 50.3 mg kg⁻¹, K 308 mg kg⁻¹, and water holding capacity 21.8%. Site3 was a farmer's field, different for lines (Giannitsa: 40°42' N, 22°24' E, 1 m asl) and hybrids (Serres: 41°01' N, 23°36' E, 15 m asl). Climatic data across growing seasons and locations are provided in Table 1. These locations are part of the major maize belt in Greece, with Site2 being almost marginal due to the high altitude associated with cool summers and the length of growing season marginally sufficient for long-season hybrids. Nitrogen and P fertilizers were applied at planting at actual amounts of 120 and 60 kg ha⁻¹, respectively, while additional N (100 kg ha⁻¹) was top-dressed when plants reached 50 cm in height. Complete weed control was obtained by tilling and hand weeding.

To preclude interplant competition and allow PYE to be fully expressed, ultra low density of 0.74 plants m⁻² was achieved (hereafter low-density regime), with individual plants occupying equidistant hills (125 cm) in a zig-zag pattern. The low-density trials were composed of 40 plants from each genotype evenly and systematically allocated, according to the replicated 31-honeycomb design (Fasoula and Fasoula, 2000; Fasoula and Tokatlidis, 2012). The dense-stand plots were established in randomized complete blocks and replicated twice, comprising two rows 4 m in length and 75 cm apart. Under normal irrigation, the in-row interplant distances were 20 and 17 cm for lines (66,666 plants ha⁻¹) and hybrids (78,431 plants ha⁻¹), respectively, with the latter population density approximating that commonly used by farmers. In deficit irrigation treatments, the in-row distance was 30 cm (44,444 plants ha⁻¹) for both lines and hybrids. The lower density was chosen in water shortage conditions to be consistent with the fact that lower densities are required for dryland compared to irrigated maize (Norwood, 2001; Blumenthal et al., 2003; Shanahan et al., 2004; Duvick, 2005; Berzsenyi and Tokatlidis, 2012). The density treatments were overplanted and thinned after emergence to the desired stand. Planting occurred from mid-April until early May.

At each site, the low-density and dense-stand trials were established twice, corresponding to the two irrigation treatments (normal = full irrigation treatment and deficit = 50% of the normal). Up to vegetative stage V6–7, both irrigation treatments received 50 mm of water for seedling establishment and early plant growth, with different irrigation levels applied thereafter. A drip-irrigation water supply system of 4 L h⁻¹ was established along every other plant row, with emitters spaced at 33 cm intervals. Irrigation scheduling was based on maize evapotranspiration (ET_c) and was applied when the crop evapotranspiration

Table 1. Climatic data including monthly mean temperature, total rainfall, potential evapotranspiration, and growing degree days (base temperature 10°C) across the three sites during the growing seasons of 2012 for lines and 2013 for hybrids.

| Season | Site1 | | | | | | | | Site2 | | | | | | Site3 | | | | | | | |
|--------|---|-------|-------|-------|-------|-------|------|------|-------|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|------|--|
| | Apr. | May | June | July | Aug. | Sept. | Oct. | Apr. | May | June | July | Aug. | Sept. | Oct. | Apr. | May | June | July | Aug. | Sept. | Oct. | |
| | <u>Mean temperature, °C</u> | | | | | | | | | | | | | | | | | | | | | |
| 2012 | 15.1 | 19.7 | 26.6 | 29.7 | 28.0 | 23.3 | 20.3 | 10.8 | 14.3 | 20.7 | 23.9 | 22.2 | 17.8 | 13.3 | 14.8 | 19.2 | 25.8 | 28.0 | 27.0 | 22.5 | 19.4 | |
| 2013 | 15.3 | 22.0 | 24.8 | 26.9 | 27.7 | 22.8 | 17.1 | 11.9 | 16.1 | 18.7 | 21.0 | 22.0 | 16.7 | 8.2 | 14.1 | 21.8 | 23.6 | 26.1 | 27.2 | 16.3 | 9.2 | |
| | <u>Total rainfall, mm</u> | | | | | | | | | | | | | | | | | | | | | |
| 2012 | 52.6 | 59.6 | 7.4 | 0.0 | 4.6 | 52.6 | 12.4 | 42.4 | 9.0 | 8.6 | 15.6 | 25.2 | 11.8 | 124.2 | 51.6 | 93.2 | 3.6 | 16.2 | 5.0 | 29.2 | 40.0 | |
| 2013 | 11.0 | 7.4 | 16.2 | 70.2 | 11.8 | 11.0 | 7.4 | 25.4 | 78.4 | 81.6 | 12.4 | 8.2 | 8.8 | 35.4 | 9.2 | 4.8 | 58.1 | 49.5 | 0.4 | 13.4 | 8.6 | |
| | <u>Potential evapotranspiration, mm</u> | | | | | | | | | | | | | | | | | | | | | |
| 2012 | 84.5 | 116.5 | 171.8 | 176.9 | 147.9 | 95.6 | 81.4 | 81 | 99.2 | 120 | 161.2 | 130.2 | 84 | 54 | 80.5 | 108.5 | 165.8 | 181.9 | 154.6 | 95.6 | 81.4 | |
| 2013 | 87.9 | 135.0 | 161.9 | 168.7 | 144.5 | 103.0 | 92.3 | 84 | 102.3 | 105 | 130.2 | 127.1 | 84 | 42 | 74.3 | 114.2 | 145.4 | 151.8 | 132.2 | 96.3 | 73.9 | |
| | <u>Growing degree days</u> | | | | | | | | | | | | | | | | | | | | | |
| 2012 | 172 | 304 | 442 | 515 | 489 | 391 | 211 | 86.2 | 166 | 316 | 387 | 352 | 266 | 184 | 245 | 345 | 465 | 490 | 510 | 398 | 310 | |
| 2013 | 184 | 357 | 414 | 478 | 488 | 382 | 198 | 93.6 | 117 | 269 | 336 | 366 | 243 | 157 | 176 | 355 | 384 | 446 | 453 | 365 | 186 | |

rate ET_c -P (rainfall) reached 50 mm. Soil water content at this level was approximately 70% of field capacity, which is considered adequate for plant growth during all stages. The ET_c was calculated from climatic parameters measured daily from meteorological stations located adjacent to each experimental site and was used to calculate the reference evapotranspiration rate (ET_o) using the Penman–Monteith method (Allen et al., 1998). The ET_c , which is the product of ET_o and the crop coefficient (K_c), was calculated using values for maize K_c adjusted to Greek conditions ($K_{cini} = 0.50$, $K_{cmid} = 1.05$, and $K_{cend} = 0.15$) for growth stages of 30/70/120/150 d after emergence (Papazafiriou, 1996; Georgiou et al., 2010; Lekakis et al., 2011).

For hybrids under both density regimes at Site1 and Site2, A and T were measured simultaneously using a portable open gas exchange system (LI-6400 XT, Li-Cor, Lincoln, NE) at a photosynthetic photon flux density >1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Leaf gas exchange was measured on the upper-most ear leaf twice, 1 wk after silking and 2 wk later during the grain-filling period. Measurements were performed on six plants from each plot from 0900 to 1200 h in the morning to avoid high vapor-pressure deficit and photoinhibition at midday. Photosynthetic WUE was calculated as the ratio of A to T (Polley, 2002; Tambussi et al., 2007). The ASI was calculated as the difference between silking date (planting to the time at which the first silks were visible and 2 cm in length on 50% of plants on each plot) and anthesis date (planting to the time at which 50% of plants per plot were shedding pollen) (Bolanos and Edmeades, 1996). The HI was determined as the ratio of grain weight to total aboveground plant weight at physiological maturity.

At low density, plants were harvested individually. Thus, grain yield was recorded at the per-plant basis and analyzed by the JMP.7 software tailored to honeycomb designs (Mauroumoustakos et al., 2006). At the dense-stand trials, grain yield was recorded at per area (plot) basis, and the MSTAT-C software was used for the three-factor (three locations, two water regimes and 30 or 31 genotypes) ANOVA. The analysis was based on the linear model and involved three fixed effect factors: locations as main plots, water regimes as subplots and genotypes as sub-subplots. The ANOVA also was applied to WUE, ASI, and HI in both density regimes. For all statistical analyses, a probability level of 0.05 was used as a baseline for significance.

Correlation analyses were conducted to determine the relationships between the six environments within each density regime as a measure of the $G \times E$ interaction as well as the

Table 2. Degrees of freedom (df) and mean square (MS) values from ANOVA as randomized complete block design for location with water regime (irrigation) as split plot on location and genotype as split plot on water regime, concerning grain yield (Mg ha^{-1}) of 30 lines and 31 hybrids at the dense-stand plots.

| Source of variation | Lines | | Hybrids | |
|---------------------|-------|---------|---------|---------|
| | df | MS | df | MS |
| Replication | 1 | 0.46 | 1 | 0.53 |
| Location (L) | 2 | 718*** | 2 | 168** |
| Error | 2 | 0.75 | 2 | 1.26 |
| Irrigation (I) | 1 | 141** | 1 | 2495*** |
| L×I | 2 | 58.7** | 2 | 114** |
| Error | 3 | 1.21 | 3 | 1.49 |
| Genotype (G) | 29 | 67.5*** | 30 | 22.3*** |
| L×G | 58 | 11.4*** | 60 | 16.3*** |
| I×G | 29 | 4.36*** | 30 | 5.58*** |
| L×I×G | 58 | 4.42*** | 60 | 4.33*** |
| Error | 174 | 0.59 | 180 | 2.12 |

** $P \leq 0.01$.

*** $P \leq 0.001$.

relationships between spaced and crowded plants to determine whether PYE is an indicator of genotype yield potential. Significant levels were categorized as weak, moderate, or strong at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively.

RESULTS

Main factors of genotype, location, and water regime, as well as their interactions were significant for both lines and hybrids at dense stand for grain yield (Table 2). As expected, normally irrigated trials averaged higher yield compared to those of deficit irrigation for both densities and both kinds of genotypes, and differences were statistically significant. When comparing low density against dense stand, water stress affected the inbred lines nearly identically, since the respective yield losses in relation to the normal irrigation were 18 and 21% (Fig. 1). Hybrid yield loss was 22% at low density and 37% (ranging from 16–51%) in the dense-stand trials. A similar pattern of water stress influence on A was shown (Fig. 1). Genotype yields across location, density and irrigation regimes are given in Supplemental Tables S1 and S2 for lines and hybrids, respectively. For lines, the across location range was 139 to 410 g plant^{-1} at low density, and 4.78 to 9.00 Mg ha^{-1} at dense stand (lowest in Site1, and highest in Site2 for both densities). For hybrids, at low-density Site1 yielded the lowest (751 plant^{-1}) and Site2 the highest (1205 g plant^{-1}) while

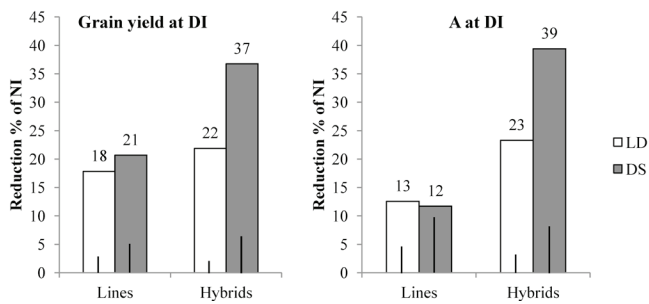


Fig. 1. The across-location influence of deficit irrigation (DI) on grain yield and assimilation rate (A) relative to normal irrigation (NI). Baseline values for grain yield are 269 g plant⁻¹ at low density and 7.15 Mg ha⁻¹ at dense stand; for A at low density (LD) and dense stand (DS), values were 22.5 and 21.2 for lines, and 27.1 and 23.1 for hybrids, respectively. Bar within each column reflects the respective LSD.

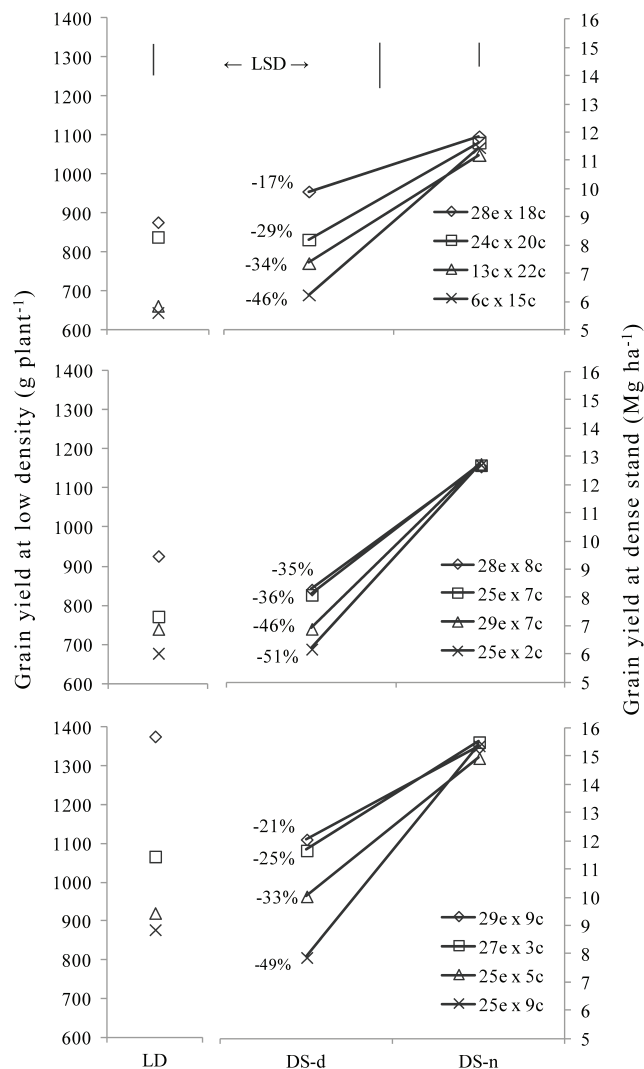


Fig. 2. Yield performance of hybrids grouped by yield potential in well-irrigated dense-stand plots (DS-n) demonstrates the beneficial effects of the improved plant yield efficiency (low density [LD]) to cope with the water deficit situation in dense stand (DS-d). Percentages at DS-d denote yield loss relative to DS-n. The LD yields are over the three locations and the two water regimes, while those of DS-d and DS-n are over the three locations. The three least significant difference (LSD) bars from left to the right correspond to comparisons between: individual hybrids within and across groups at LD, individual hybrids within and across groups at DS-d and/or DS-n, and the three group means in the DS-n.

Table 3. Simple correlation coefficients among the six low-density (LD) environments for grain yield under normal irrigation (NI) and deficit irrigation (DI) across three sites.

| LD environment | LD | | | | |
|------------------------------|-----------|-----------|-----------|-----------|-----------|
| | Site3(DI) | Site3(NI) | Site2(DI) | Site2(NI) | Site1(DI) |
| Inbred lines (n = 30) | | | | | |
| Site1 (NI) | 0.91*** | 0.86*** | 0.86*** | 0.86*** | 0.94*** |
| Site1 (DI) | 0.92*** | 0.90*** | 0.87*** | 0.88*** | |
| Site2(NI) | 0.88*** | 0.90*** | 0.94*** | | |
| Site2(DI) | 0.83*** | 0.86*** | | | |
| Site3(NI) | 0.94*** | | | | |
| Hybrids (n = 31) | | | | | |
| Site1 (NI) | 0.77*** | 0.64*** | 0.73*** | 0.77*** | 0.85*** |
| Site1 (DI) | 0.72*** | 0.64*** | 0.69*** | 0.70*** | |
| Site2(NI) | 0.83*** | 0.76*** | 0.92*** | | |
| Site2(DI) | 0.70*** | 0.62*** | | | |
| Site3(NI) | 0.90*** | | | | |

*** $P \leq 0.001$.

at dense-stand Site2 gave the lowest yield (9.81 Mg ha⁻¹) and Site3 the highest (11.77 Mg ha⁻¹). Line 31c averaged the lowest yield in both density regimes (102 g plant⁻¹, and 3.16 Mg ha⁻¹), while the highest yielding lines were 26e and 25e at low density (631 plant⁻¹) and at dense stand (13.76 Mg ha⁻¹), respectively. Hybrid 6c × 15c was the lowest yielding (637 plant⁻¹ and 8.85 Mg ha⁻¹), while hybrid 29e × 9c the highest yielding (1358 g plant⁻¹ and 13.71 Mg ha⁻¹).

Yield loss at the water deficit vs. the well-irrigated dense stand was significant for all the hybrids except one (LSD = 1.67 Mg ha⁻¹). When yield loss was paired with the respective overall genotype grain yield at low density (i.e., PYE), there was a tendency for negative correlation ($r = -0.31$, $P \leq 0.10$). This negative correlation is further demonstrated in Fig. 2, where 12 line single-crosses are grouped by their grain yield plateau at well-irrigated dense stand. In terms of the lowest-yielding group (11.50 Mg ha⁻¹), the hybrid 28e × 18c of 880 g PYE lost 17% (not significant); yield loss of the remaining three hybrids was up to 46% for hybrid 6c × 15c of the lowest PYE (645 g). Yield-loss ranges of 35 to 51% and 21 to 49% for groups of intermediate- and highest-yield plateau, respectively, also were inversely associated with PYE.

The hybrids differed significantly for HI, WUE, and ASI measured in the DS trials, and the across-two location overall values were 0.35 to 0.45, 5.27 to 6.50, and -0.9 to 4.8 d, respectively. Water stress decreased more drastically for ASI by delaying by 60% the silk emergence compared to the WUE (about 15% lower), while HI was similar at the two water regimes (data not shown). There was no correlation between HI with hybrid yield performance at low density, while WUE and ASI correlated with PYE, the former directly proportional ($r = 0.62$, $P \leq 0.001$) and the latter inversely proportional ($r = -0.47$, $P \leq 0.01$).

At low density, all simple correlation values (r) among the six environments for grain yield per plant were greater than 0.62 and were strongly significant (Table 3). In the dense-stand trials, 3 out of the 15 correlations were not significant for the inbred lines, while three, four, and five correlations exhibited weak, moderate, and strong significance, respectively (Table 4). The significant hybrid × location interaction in the dense-stand

Table 4. Simple correlation coefficients among the six dense-stand (DS) environments for grain yield under normal irrigation (NI) and deficit irrigation (DI) across three sites.

| DS | | | | | |
|-----------------------|-----------|-----------|-----------|-----------|-----------|
| Environment | Site3(DI) | Site3(NI) | Site2(DI) | Site2(NI) | Site1(DI) |
| Inbred lines (n = 30) | | | | | |
| Site1 (NI) | 0.54** | 0.43* | 0.34ns† | 0.59*** | 0.46* |
| Site1 (DI) | 0.50** | 0.40* | 0.26ns | 0.34ns | |
| Site2(NI) | 0.52** | 0.56** | 0.65*** | | |
| Site2(DI) | 0.65*** | 0.76*** | | | |
| Site3(NI) | 0.88*** | | | | |
| Hybrids (n = 31) | | | | | |
| Site1 (NI) | 0.30ns | 0.16ns | 0.23ns | 0.29ns | 0.53** |
| Site1 (DI) | 0.33ns | 0.03ns | 0.05ns | 0.16ns | |
| Site2(NI) | 0.17ns | 0.26ns | 0.29ns | | |
| Site2(DI) | 0.21ns | 0.04ns | | | |
| Site3(NI) | 0.57** | | | | |

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

† ns, not significant.

trials was attributable to the different genotype rank, as just 2 out of the 15 r values were significant.

The correlation of genotype yield performance between the two planting density regimes is illustrated in Table 5. For the inbred lines, when grain yield at a particular environment under the low density was paired with grain yield at the six environments under the dense stand, all r values were significant. Twenty-four out of the 36 such correlations denoted strong relationships, while the six involving Site1 under deficit irrigation were weak and at normal irrigation were mostly moderate. Strong correlation was found when the over-location and water regime genotype yield at low density was compared with the respective factor in the dense stand ($r = 0.90$). For the hybrids, 14 correlations were not significant, while 13 were weak, 4 were moderate, and 5 were strong. The over-location and water regime correlation was strongly significant ($r = 0.70$).

Table 6. Simple correlation coefficients of the overall grain yields in the dense-stand (DS) trials with each of the six environments across the two density regimes under normal irrigation (NI) and deficit irrigation (DI) across three sites.

| Environment | Inbred lines (n = 30) | | Hybrids (n = 31) | |
|-------------|-----------------------|-------------|------------------|-------------|
| | Low density | Dense stand | Low density | Dense stand |
| Site1 (NI) | 0.81*** | 0.68*** | 0.58*** | 0.67*** |
| Site1 (DI) | 0.85*** | 0.59*** | 0.59*** | 0.56** |
| Site2(NI) | 0.87*** | 0.78*** | 0.67*** | 0.51** |
| Site2(DI) | 0.84*** | 0.80*** | 0.68*** | 0.39* |
| Site3(NI) | 0.88*** | 0.90*** | 0.58*** | 0.68*** |
| Site3(DI) | 0.90*** | 0.89*** | 0.64*** | 0.77*** |

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

Assuming the average yield in the dense-stand trials across the six trials as an index of genotype crop yield potential, Table 6 illustrates its correlations with each individual trial. Regarding the inbred lines, both density regimes showed strongly significant correlations. The low-density trials of the hybrids also exhibited strongly significant correlations. For the hybrids at the dense-stand trials, one correlation was weak, two correlations were moderate, and three were strongly significant.

Mid-parent yield was measured as possible indicator of the hybrid performance. It showed a consistently significant correlation with hybrid yield at low density, that is, r values of 0.70 ($P \leq 0.001$), 0.49 ($P \leq 0.001$), and 0.53 ($P \leq 0.001$) for Site1, Site2, and across-three-location estimations, respectively. At the dense-stand trials, correlation was significant but negative for Site1 ($r = -0.45$, $P \leq 0.05$) and not significant for Site2 and across-location estimations.

DISCUSSION

Water stress exerted a more drastic effect in the dense-stand compared to the low-density trials regarding yield and assimilation rate (Fig. 1). Several investigations have indicated that

Table 5. Simple correlation coefficients of the six low-density (LD) environments with the six dense-stand (DS) environments for grain yield under normal irrigation (NI) and deficit irrigation (DI) across three sites. Overall correlations are between the over-LD and over-DS yields.

| LD/DS | Site3(DI) | Site3(NI) | Site2(DI) | Site2(NI) | Site1(DI) | Site1(NI) |
|-----------------------|-----------|-----------|-----------|-----------|-----------|-----------|
| Inbred lines (n = 30) | | | | | | |
| Site1 (NI) | 0.77*** | 0.80*** | 0.65*** | 0.59*** | 0.39* | 0.53** |
| Site1 (DI) | 0.81*** | 0.88*** | 0.71*** | 0.55** | 0.40* | 0.54** |
| Site2(NI) | 0.81*** | 0.82*** | 0.63*** | 0.73*** | 0.39* | 0.58*** |
| Site2(DI) | 0.76*** | 0.79*** | 0.64*** | 0.66*** | 0.41* | 0.53** |
| Site3(NI) | 0.83*** | 0.89*** | 0.74*** | 0.70*** | 0.43* | 0.54** |
| Site3(DI) | 0.84*** | 0.89*** | 0.71*** | 0.59*** | 0.40* | 0.57** |
| Overall | 0.90*** | | | | | |
| Hybrids (n = 31) | | | | | | |
| Site1 (NI) | 0.41* | 0.27ns† | 0.35 ns | 0.14ns | 0.33ns | 0.62*** |
| Site1 (DI) | 0.31ns | 0.30ns | 0.32 ns | 0.24ns | 0.34ns | 0.63*** |
| Site2(NI) | 0.40* | 0.37* | 0.36* | 0.41* | 0.33ns | 0.61*** |
| Site2(DI) | 0.40* | 0.48** | 0.31ns | 0.40* | 0.31ns | 0.57*** |
| Site3(NI) | 0.50** | 0.18ns | 0.36* | 0.37* | 0.40* | 0.45* |
| Site3(DI) | 0.50** | 0.14ns | 0.44* | 0.37* | 0.46** | 0.61*** |
| Overall | 0.70*** | | | | | |

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

† ns, not significant.

modern hybrids suffer severely from inadequate water supply at normal densities required in seasons with adequate rainfall (Norwood, 2001; Kiniry et al., 2002; Blumenthal et al., 2003; Shanahan et al., 2004). Therefore, when drought prevails, lower populations are indispensable for ensuring survival and accomplishment of seasonal yield potential (Duvick, 2005; Berzsenyi and Tokatlidis, 2012). In a recent review, it was demonstrated that interseasonal variation in optimum population density implies ineffective resource use, and data from two field investigations revealed potential crop disaster for a dry season under the required population for a favorable season (Tokatlidis, 2013). Hence, the highly differential hybrid response to water deficit, and the sign of negative association between PYE and yield loss due to water shortage (Fig. 2) indicate that there is room for breeding toward better adaptation to rainfed production systems. Absence of tight connection between PYE and yield loss was a reasonable outcome given the variety of hybrid yield potential. Nevertheless, comparison of the two hybrids of lowest and highest PYE ($6c \times 15c$ and $29e \times 9c$), indicates substantially less yield loss for the latter, even though of higher yield potential under adequate water supply (Fig. 2). It is clear that yield capacity at the single-plant level is a key element to succeed in better adaptation in environments prone to drought, as experimental data have shown (Berzsenyi and Tokatlidis, 2012), and the recent review sedulously documented it (Tokatlidis, 2013). Duvick (2005) noted that improved yield capacity at the single-plant level might be practical for hybrids suited for drought-prone environments, where planting at lower populations is prudent but the ability to utilize occasional higher rainfall by increasing yield per plant would be desirable. The climate change scenarios include an increase in seasonal drought intensity (Cairns et al., 2013), so the differential response of maize hybrids to spatial and temporal heterogeneity (Williams et al., 2008) might be exploited to isolate those less vulnerable to the huge environmental diversity (Tokatlidis, 2013).

Differential hybrid performance for gas exchange WUE at normal densities and positive correlation with PYE was also encouraging. Driever et al. (2014) suggested that natural variation in photosynthetic capacity is a currently unexploited genetic resource and could be used for potential crop improvement (Lawson and Blatt, 2014; Tardieu et al., 2014; Ge et al., 2012). Synchronization of pollen and silk emergence is presumably important under water stress conditions; thus, the negative relationship of PYE with ASI also supports this. The strong negative relationship between these traits has been reported by Menkir and Kling (2007) and Greveniotis et al. (2012). Bridging the anthesis to silking gap was deemed essential to avoid abortion and improve kernel set and yield (Cárcova et al., 2000; Monneveux et al., 2006; Carena et al., 2009).

The source of the $G \times E$ interaction was substantially different across the two density regimes. At low density, accounting for the large across-location differences (Supplemental Tables S1 and S2) by the relationships of strength among environments (Table 3), this interaction can be considered quantitative rather than qualitative. The quantitative part is nearly inevitable due to temporal and spatial variation induced by soil, climatic, and other (i.e., pests) parameters. Conversely, in the dense-stand trials, both types of $G \times E$ interaction were

present, particularly for the hybrids whose ranks across environments were inconsistent (Table 4). Hence, the low-density regime seems to have succeeded in a higher degree of heritability for both lines and hybrids, particularly for the latter. The absence of interplant competition also negated confounding quantitative or crossover interactions, which is exceptionally beneficial for identifying superior genotypes. These findings agree with the evidence showing that the absence of competition ensures higher heritability compared to competition (Kyriakou and Fasoulas, 1985; Tokatlidis et al., 2010a; Fasoula and Tokatlidis, 2012). Rosielle and Hamblin (1981) speculated that genetic variance in stress environments is generally lower than that in non-stress environments. Mansfield and Mumm (2014) also found the importance of $G \times E$ interaction to increase and the narrow-sense heritability for grain yield to decline consistently with intensifying density and environmental stress.

Regarding the possibility of genotype selection in space-planted nurseries to ensure good performance in normally seeded situations, data from Table 5 illustrate a split outcome. With respect to inbred lines, correlations showed a near-perfect match for Site2 and Site3 and a fairly strong one for Site1. Regarding hybrids, half of the correlations denoted lack of predictability. This split outcome could be attributed to the lower degree of heritability attained by the hybrids in the dense-stand trials. Regarding hybrids vs. lines in the dense-stand trials (Table 4), the near absolute absence of significant correlation among the six environments reflected a substantially lower degree of heritability for the former. Nonetheless, crop yield potential was reflected more from the overall hybrid performance in the dense stand (i.e., averaged across the six environments); it was significantly correlated with both the overall hybrid performance at low density (Table 5) or the hybrid performance at each low-density trial (Table 6). These results agree with those reported by Hansen et al. (2005) in wheat, who found lower correlations when space-planted means were paired with yield in a solid-seeded situation from 1 yr but high correlations with densely seeded plots weighted across four environments. The authors noted that a realistic scenario involves selection in space-planted nurseries in only one trial for subsequent performance in multiple environments, in agreement with the results of the present study.

Lower degree of heritability attained by hybrids in the dense-stand trials also accounts for better prediction of the yield potential of the lines compared to that of the hybrids (Tables 5 and 6). It is important to note that yield potential was better predicted by the low-density rather than the dense-stand trials, and particularly for the lines. Regarding hybrids, each individual low-density trial also exhibited a significant correlation (Table 6), while, overall, low-density regime exhibited strong correlation (Table 5). Consequently, performance at the low density cannot be overlooked as a potentially prognostic tool of genotype yield potential at farming densities. These results corroborate with similar results in maize (Tokatlidis et al., 2011) and in other crops (Ntanos and Roupakias, 2001; Tokatlidis et al., 2010b; Vlachostergios et al., 2011; Kargiotidou et al., 2014).

This study placed particular emphasis on individual plant yield performance as an indicator of hybrid performance at typical farming density conditions. The results suggest that improved PYE is an essential agronomic element for dryland

maize production. Therefore, from a breeding perspective, potential association of lines and hybrids for PYE is a reasonable query. Even though they should be considered with great caution since parents and hybrids were evaluated in different seasons, the low-density trials indicated positive correlation between mid-parent and hybrid yield. This was not true for the dense stand where the opposite inference was drawn from Site1. Accounting for higher degree of heritability accomplished at low density, the first rather than the second inference seems more realistic. If this is the case, these results emphasize the additive gene action at densities assumed to be non-stress conditions, and selection for line yield per se might be promising as previous studies showed (Tokatlidis et al., 1999; Fasoula and Tollenaar, 2005; Greveniotis et al., 2012). Analysis of gene action for grain yield across plant densities by Mansfield and Mumm (2014) emphasized the prominence of additive gene action at lower rather than at higher densities. Mounting evidence indicates that additive is the predominant type of gene action in the expression of yield and other quantitative traits (Crow, 2000; Butruille et al., 2004; Troyer and Wellin, 2009).

In terms of the initially established queries, the results suggest that yield of space-planted environments can be transferred to densely seeded situations. Performance of hybrids suggests PYE as an indispensable agronomic trait that advances adaptation to water-deficit conditions; in concordance were correlations of PYE with WUE and ASI. Improved hybrid PYE was connected with improved parent PYE mainly exhibited by the experimental lines. Low-density regimes necessary to breed for PYE were found to lighten the implications of $G \times E$ interactions.

CONCLUSIONS

Improved PYE could contribute to versatile hybrids that are adaptable to environmental heterogeneity, which are clearly desirable for coping with climatic changes expected to intensify drought events. The PYE, fully expressed in ultra-spaced plants, optimizes heritability and is devoid of confounding crossover types of $G \times E$ interaction, therefore constituting a criterion for dependable selection and evaluation. Improved yield at the single-plant level does not compromise per-area yield potential but instead constitutes an added value in terms of the across-density and environment stability. It appears that very low-density conditions accentuate the additive genetic variance, opening the possibility of alleviating the yield gap between hybrids and parents.

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