Maize Stand Density Yield Response of Parental Inbred Lines and Derived Hybrids

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ABSTRACT

Maize (*Zea mays* L.) grain yield has a parabolic response to stand density changes, creating an optimum stand density that maximizes yield. Argentinean commercial hybrids differ in their optimum stand density when grown at similar environments, generating the need to test precommercial hybrids for adequate product management recommendations. For breeding purposes, any information from parental inbred lines that is indicative of derived hybrid performance is highly desirable. However, correlations between parental inbred line and derived hybrid performance for maize yield response to stand density are unknown. We characterized a set of maize inbred lines and derived single cross hybrids (9 female and 5 male inbreds, 42 hybrids) during two growing seasons for their yield response to stand density to evaluate the correlation between parental inbred line and derived hybrid performance. Significant ($p < 0.01$) hybrid differences were found for yield at different stand densities, optimum stand density, and yield at optimum stand density. However, correlations between parental inbred line and derived hybrid performance were not significant for optimum stand density. Despite the lack of correlation, specific parental inbreds producing hybrids with higher optimum stand density or higher yield at optimum stand density were evident. Our results indicate that pedigree information, more than the specific inbred response to stand density, is relevant for estimating derived hybrid stand density yield response.

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Abbreviations: GCA, general combining ability; MPH, midparental heterosis; OSD, optimum stand density; SCA, specific combining ability.

A STEADY INCREASE in stand density has been a relevant driver of maize-yield improvements during the hybrid era (Duvick et al., 2004; Egli, 2015). At the farmers' level, correct stand density management is critical for maximizing maize grain yield. Contrary to most crops, maize yield shows a parabolic response to stand density changes (Echarte et al., 2000; Sangoi et al., 2002; Sarlangue et al., 2007), where yield is maximized at a particular optimum stand density (OSD). It is widely known by crop managers, physiologists, and breeders that this OSD varies with the environment (e.g., N and water availability). Higher-yielding environments have maximum yields at higher stand densities (Al-Kaisi and Yin, 2003; Berzsenyi and Tokatlidis, 2012), generating the need to decide which stand density is needed at each particular situation (Reeves and Cox, 2013; Van Roekel and Coulter, 2011, 2012; Robles et al., 2012). Recent evidence has also shown that large genotype × stand density interactions are evident at some production regions, creating the need for farmers to decide stand densities not only based on the environment, but also on the particular genotype they are sowing. Commercially available hybrids differ in their OSD for similar environments in central Argentina (Sarlangue et al., 2007; Hernández et al., 2014), and seed companies are providing farmers with genotype-specific information for stand density management.

Recent studies conducted at the inbred level on the genetic basis of traits related to stand density response (Gonzalo et al., 2010) showed that genetic control of stand density response is multigenic, and that additive effects, as well as epistatic interactions, are relevant. For breeding purposes, trait evaluation at the inbred level has little value if the parental inbred performance is not correlated to the derived hybrid performance (Hallauer et al., 2010). Any information on parental inbred lines that is indicative of derived hybrid performance is highly desirable for eliminating the need to conduct large-yield trials. Studies over traits such as grain yield, plant height, and prolificacy have shown correlations between parental inbred lines and derived hybrid performance to be generally low (Hallauer et al., 2010). This is explained by the high phenotypic plasticity and significant environmental modulation of these traits, which is reflected in their low heritability (Sadras and Slafer, 2012).

There is evidence of a high correlation between parental inbred line and derived hybrid performance for traits that have higher heritability than yield, like traits related to grain filling (Alvarez Prado et al., 2013) or to plant development (D'Andrea et al., 2013). At present, correlations between parental inbred line and derived hybrid performance for yield responses to stand density are unknown. This information is useful for determining the value of studying stand density responses at the inbred level and their possible use as indicators of future hybrid performance.

Maize grain yield response to stand density changes is usually dissected into two components: potential yield per plant and tolerance to crowding stress. The latter component has been successfully increased by breeding and is responsible for most yield improvements (Russell, 1968, 1991; Duvick and Cassman, 1999; Tollenaar and Wu, 1999; Sangoi et al., 2002; Duvick et al., 2004; O'Neill et al., 2004; Tokatlidis and Koutroubas, 2004; Egli, 2015). There is conflicting evidence about the first component, however. Some studies have shown that potential yield per plant has increased (Luque et al., 2006; Ci et al., 2011), while others have described that it has remained mostly stable (Duvick and Cassman, 1999; Tollenaar and Wu, 1999; Sangoi et al., 2002; Duvick et al., 2004). It is widely accepted that the higher crowding tolerance of modern genotypes has increased the stand density that farmers are using. However, the response of parental inbred lines to stand density and the correlation between parental inbred line and derived hybrids for crowding tolerance and potential yield per plant are unknown.

Our general objective was to test if information related to stand density yield response at the inbred level can help predict derived hybrid responses. Specific objectives were (i) to characterize a set of maize inbred lines and derived single-cross hybrids for their stand density yield response, and (ii) to evaluate the correlation between parental inbred line and derived hybrid performance for their OSD.

MATERIALS AND METHODS
Site and Crop Management
Experiments were conducted at the Campo Experimental Villarino located in Zavalla (33°1′ S, 60°53′ W), Santa Fe, Argentina, during 2012–2013 (year one) and 2013–2014 (year two). Sowing dates were 27 Sept. 2012 and 30 Sept. 2013. Both experiments were planted under no tillage management, and the previous crop was always soybean [*Glycine max* (L.) Merr.]. Fertilizer (20–0–0–16, N–P–K–S) was broadcasted 4 to 5 d before sowing with a rate of 100 kg N ha⁻¹, and monoammonium phosphate (MAP, 10–50–0–0) was applied at sowing with a rate of 20 kg N ha⁻¹. Experiments were rainfed and conducted without important visible water limitations. Weeds were controlled using standard agronomic practices and manually removed whenever necessary.

Rainfall from sowing date to physiological maturity was different across years. Both years showed similar rainfall distribution, but the total rainfall amount was quite different (681 and 390 mm for years one and two, respectively). During the flowering period (about 30 d bracketing flowering) rainfall was 217 and 83 mm for years one and two, respectively. Average temperatures were also different (21.5 and 22.8°C for years one and two, respectively), making year two a warmer and dryer growing season.

Plant Material and Experimental Design
Nine female inbreds, five male testers, and 42 derived single-cross hybrids from Nidera S.A. were evaluated (Table 1). All inbred lines were elite lines from the company, and several crosses were commercially available hybrids at the time the study was conducted. Genotypes were all evaluated in two growing seasons, except hybrid M4 × F3, which was only evaluated during year one, and hybrids M4 × F1 and M4 × F2, which were only evaluated during year two.

All genotypes were tested at three stand densities: low, intermediate, and high (1, 8, and 16 plants m⁻², respectively). The purpose was not to have a large number of stand densities but to use contrasting stand densities so that isolated plants, as well as plants under severe stress, were considered in the analysis.

Experiments were arranged using a split-split-plot design with three replicates in randomized complete blocks, with stand

Table 1. List of female inbreds, male testers, and derived hybrids.

| Female inbreds | Male testers | | | | |
| | M1 | M2 | M3 | M4 | M5 |
	2NE58	2SE88	ITMG2HE75	TDM2NE63	ITMG8BX28
F1 1TH06	×	×	×	×	×
F2 7RE23	×	×	×	×	×
F3 7TE98	×	×	×	×	×
F4 7UB02	×	×	×	×	×
F5 7UE44	×	×	×	×	×
F6 IT7SE24	×	×	×	×	×
F7 7TE24	×	×	×	×	
F8 7UE12	×	×	×	×	
F9 7UE76	×	×	×	×	

density as main plots, type (inbred lines or hybrids) as subplots, and genotypes within type (inbreds or hybrids) as sub-subplots (hereafter termed plots). Plots were six rows for the lowest stand density and four rows for intermediate and high stand densities. Plots were 6 m long and rows were 0.52 m apart, while plant-to-plant distance on the row was 1.92, 0.24 and 0.12 m for the low, intermediate, and high stand densities, respectively. Plots were overplanted and manually thinned at V2 to V3 ligulated leaves (Ritchie et al., 1993).

Phenotypic Measures

Yield was determined after harvesting all ears from the two central rows at the intermediate (8 plants m^{-2}) and high (16 plants m^{-2}) stand densities and from the four central rows at the lowest one (1 plant m^{-2}) after physiological maturity. Yield values were corrected and reported using 145 g kg^{-1} moisture. Following Tollenaar (1989) and Hernández et al. (2014), OSD was estimated by adapting the equation proposed by Duncan (1958) (Eq. [1]):

$$OSD = -1/(0.932b) \quad [1]$$

The parameter b of the equation is the slope of linear regression (Eq. [2]). The original constant was changed from 2.303 to 0.932 to transform data from plants ha^{-1} to plants ac^{-1}. Reliability of the equation proposed by Duncan (1958) has been documented in Tokatlidis (2013), and we accordingly verified this by using data from Hernández et al. (2014) and Sarlangue et al. (2007) (not shown). A linear regression model was fit for each genotype × year × replicate combination to relate natural logarithm of individual plant yield (ln$y$) with stand density (Duncan, 1958) (Eq. [2]) using Graph Pad Prism V5.0 (GraphPad Software, 2007). The r^2 values ranged from 0.77 to 0.99. Replicates were used for an ANOVA test:

$$\ln y = a + bx \quad [2]$$

Individual plant yields were estimated using the ln$y$ values (Eq. [3]), and crop yield at OSD (Y_{OSD}) was estimated as the product between individual plant yield at OSD (y_{OSD}) and estimated OSD (Eq. [4]):

$$y_{OSD} = \exp^{\ln y} \quad [3]$$

$$Y_{OSD} = OSD \times y_{OSD} \quad [4]$$

Statistical Analysis

Analysis of variance was conducted for yield, OSD, and yield at OSD using generalized linear models with the GLM procedure of SAS (SAS Institute, 1999). First, inbred lines and derived hybrids were evaluated jointly. The model included environments (years), type (inbred lines or hybrids), genotypes within type, replicates (nested within year) and stand density (only for yield analysis). Means were compared with a LSD test at the 0.05 probability level.

Second, the hybrid effect was partitioned into different sources of variation. The model included environments (years), female inbred effect or general combining ability (GCA) of the female, male tester effect or GCA of the tester, interaction between female line and male tester or the specific combining ability (SCA), the interaction between female inbred and the environment, the interaction between male tester and the environment, and the interaction between female inbred, male tester, and environment effects. Also, when yield was evaluated,

stand density and the interactions with other sources of variations were considered. Means were compared with a LSD test at the 0.05 probability level.

Derived hybrids were grouped by their parental male tester or by their parental female inbred when corresponding. Best linear unbiased predictors (BLUP) of hybrids, grouped by their male tester or female inbred, were estimated. Estimations were calculated with SAS® PROC MIXED (SAS Institute, 1999).

Midparental heterosis (MPH) was calculated as the superiority of the derived hybrid compared with its midparental average (Hallauer et al., 2010):

$$MPH = [(DHM - MP)] \times 100$$

in which DHM is the derived hybrid mean and MP is the midparental value. Statistical significance of heterosis values for each trait was determined by a t-test. Correlation analyses were done by comparing the average of the two parental inbred lines and their specific testcross for each trait. The Pearson correlation coefficient r was used for establishing the association between the midparental inbred line performance and derived hybrid performance.

RESULTS
Yield Response to Stand Density Changes

There were significant yield differences ($p < 0.001$) between years, stand densities, genotype type (inbred vs. hybrids), and genotypes within type (Table 2). All interactions were also significant ($p < 0.001$), including stand density × genotype within type and year × stand density × genotype within type, showing that genotypes yielded differently at the different years and stand densities. This is in general coincident with previous studies (Sarlangue et al., 2007; Hernández et al., 2014), which show significant genotype × stand density interactions across commercial hybrids for the region.

Results also indicated that stand density did not have the same effect on yield when years were compared (Table 2). Year one showed significantly higher yields than year two. Among stand densities, the intermediate stand density showed the highest average yield during both years, except for inbred lines during year one, where maximum average yield for all inbreds was higher at the highest stand density (Table 2). As expected, inbred lines had significantly lower yields than their derived hybrids across all stand densities ($p < 0.001$). Complete yield data of all genotypes, stand densities, and years are shown as supplemental material (Supplemental Table S1).

Because we used several female inbreds and male testers, we were able to partition the different sources of variation (female inbred, male tester, and female inbred × male tester interaction) over hybrid yield performance. The contribution of the inbred line over the derived hybrid yield performance was detected with the additive (GCA) portion of the genetic variance. The nonadditive (SCA) portion of the genetic variance was estimated with the female inbred × male tester interaction, which in this case was not significant ($p > 0.05$, Table 2). A significant

male tester effect was detected ($p < 0.01$, Table 2). Also, significant interactions with year, stand density, and male tester effects were evident ($p < 0.05$), indicating that the male tester effect on yield was different across the evaluated years and stand densities (Table 2). These results showed that genetic variations in this set of inbred lines and derived hybrids could be explained by additive effects—the predictable portion of genetic variance—that also had significant interactions with the environment.

Table 2. Mean, maximum (max), and minimum (min) yields (kg ha⁻¹) at different stand densities (1, 8, and 16 plants m⁻² denoted as low, medium, and high, respectively) for inbred lines and derived hybrids evaluated in two growing seasons (years one and two). Specific yields of each inbred line or derived hybrid are available as supplemental information (Supplemental Table S1). Partitioning of total sum of squares and significance of corresponding analyses of variance are described.

Type		Stand density					
		Low		Medium		High	
		Yr 1	Yr 2	Yr 1	Yr 2	Yr 1	Yr 2
		\-\-\-\-\-\-\-\-\-\-\-\-\-\-\-\-\- kg ha⁻¹ \-\-\-\-\-\-\-\-\-\-\-\-\-\-\-\-					
Hybrids	Average	2666	2286	11671	8656	10179	7056
	Min	2164	1369	9836	7080	8201	5301
	Max	3610	3113	14414	10535	12898	8633
Inbred lines	Average	565	550	2823	2225	3032	1593
	Min	42	24	126	177	13	40
	Max	1056	973	5572	4964	6562	3138
Inbred lines and hybrids							
Year				3.3***†			
Stand density (SD)				28.8 ***			
Type				43.5 ***			
Genotype (type)				2.1 ***			
Year × SD				1.3 ***			
Year × type				0.8 ***			
SD × type				9.3 ***			
Year × genotype (type)				1.3 ***			
SD × genotype (type)				2.1 ***			
Year × SD × type				0.3 *** (414)‡			
Year × SD× genotype (type)				1.3 * (1343)			
Hybrids							
Year				8.5 ***			
SD				77.9 ***			
Female (F)				0.2			
Male (M)				0.2 **			
F × M				0.4			
Year × SD				2.9 ***			
Year × F				0.1			
Year × M				0.5 ***			
SD × F				0.3 * (462)			
SD × M				0.6 ***			
Year × SD × F				0.1			
Year× SD × M				0.2 * (487)			
Year × SD × F × M				2.0			

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

† Percentage (%) of the total sum of squares.

‡ LSD values in parenthesis ($p < 0.05$).

Genotypic Differences in Optimum Stand Density

Because genotypes showed a differential response to stand density changes, we calculated the OSD that maximized yield for each genotype evaluated at each year (Table 3). Significant differences in OSD among years ($p < 0.001$) and genotypes within type (inbreds or hybrid, $p < 0.001$) were observed.

Surprisingly, there were no significant differences in OSD when inbred lines and derived hybrids were compared, showing that inbred lines and hybrids maximized their yields at similar stand densities. The year × genotype within type interaction was significant ($p < 0.001$), showing that the genotype ranking for OSD was not the same in different environmental conditions. All genotypes exhibited an OSD that ranged from 8.0 to 14.8 plants m⁻² in year one and 7.5 to 13.8 plants m⁻² in year two (Table 3). Complete OSD data of all genotypes and years are shown as supplemental material (Supplemental Table S2).

Similar to the yield data, hybrid performance was dissected in relation to the parental inbred line (GCA) portion of the variance and the female inbred × male tester interaction, calculating the nonaddictive (SCA) portion of the

Table 3. Mean, maximum (max), and minimum (min) values of optimum stand density (OSD) and yield at OSD (Y_{OSD}) for inbred lines and derived hybrids. Specific values for each inbred line or derived hybrid are available as supplemental information (Supplemental Table S2). Partitioning of total sum of squares and significance of corresponding analyses of variance are described.

Type		OSD		Y_{OSD}	
		Yr 1	Yr 2	Yr 1	Yr 2
		\-\-\- plants m⁻² \-\-\-		\-\-\-\-\- kg ha⁻¹ \-\-\-\-\-	
Hybrids	Average	11.4	10.0	13287	9723
	Min	8.0	7.5	11240	7627
	Max	14.8	13.8	14821	11618
Inbred lines	Average	13.0	8.8	3689	2089
	Min	10.5	5.2	1245	91
	Max	18.3	18.5	5899	4148
Inbred lines and hybrids					
Year		13.1***†		16.3 ***	
Type		0.1		72.9 ***	
Genotype (type)		30.6 ***		3.2 ***	
Year × type		1.1		1.2 *** (417)	
Year × genotype (type)		18.2 *** (2.9)‡		2.1 *** (1351)	
Hybrids					
Year		11.5 ***		67.0 ***	
Female (F)		5.5 * (0.8)		1.5	
Male (M)		21.8 *** (0.6)		1.6 *	
F × M		9.9		3.9	
Year × F		1.8		0.6	
Year × M		2.1		4.4 *** (492)	
Year × F × M		4.4		3.4	

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

† Percentage (%) of the total sum of squares.

‡ LSD values in parenthesis ($p < 0.05$).

genetic variance. Optimum stand density showed no significant SCA ($p > 0.05$), and significant parental female inbred ($p < 0.05$) and male tester effects ($p < 0.001$) were detected (Table 3). Figure 1 describes the optimum stand density of the derived hybrids, grouped by their corresponding female inbred and male tester across years one and two.

Since genotypes within type showed significant differences in OSD, we calculated the yield at this specific stand density for each genotype and environment combination. This allowed us to test significant differences in yield across genotypes when they are grown at their specific OSD (Table 3). Significant differences in yield at OSD among years ($p < 0.001$), type (inbred vs. hybrids, $p < 0.001$), and genotypes within type ($p < 0.001$) were observed. The year × genotype within type interaction was significant ($p < 0.001$), as well as the year × type interaction ($p < 0.001$). These results indicated that differences among genotypes or between inbreds and hybrids were not similar across different years. Yield at OSD for inbred lines ranged from 1245 to 5899 kg ha^{-1} in year one and from 91 to 4148 kg ha^{-1} in year two, while derived hybrids ranged from 11240 to 14821 kg ha^{-1} in year one and from 7627 to 11618 kg ha^{-1} in year two (Table 3).

For estimating additive and nonadditive portions of genetic variance, hybrids were also analyzed separately for yield at OSD. A significant male tester effect ($p < 0.05$) was detected as well as a tester × year interaction effect ($p < 0.001$), but yield at OSD did not show a significant female inbred × male tester interaction effect ($p > 0.05$, Table 3).

Heterosis

As expected, yield was significantly higher in derived hybrids than in inbred lines in all stand densities and environments ($p < 0.01$). Mean parental heterosis values were 426, 391, and 389 % for 1, 8, and 16 plants m^{-2} stand densities, respectively (Table 4).

When evaluating OSD, there were no significant differences between inbred lines and derived hybrids,

Table 4. Mean parental heterosis (MPH) for yield at different stand densities (1, 8, and 16 plants m^{-2}) for two growing seasons (years one and two).

Stand density plants m^{-2}	MPH	Range	Year 1 MPH	Year 2 MPH
			%	
1	426	212–943	455***	396***
8	391	121–1156	390***	391***
16	389	124–887	315***	463***

*** $p < 0.001$.

resulting in no heterosis for this trait. On the other hand, when yield at OSD was evaluated, significant differences were found among inbred lines and hybrids. Mean parental heterosis values were 330 and 470% for years one and two, respectively (Table 5).

Correlation Analysis

We tested if derived hybrid performance was correlated to the midparental inbred line performance for all evaluated traits. The midparental inbred line performance is the average between the female and male parents of the derived hybrid. Yield data were grouped by year and stand density, and correlations were not significant for any combination (data not shown).

Optimum stand density and yield at OSD did not show significant correlations between midparental inbred line and derived hybrid performance. The only exception was OSD in year two, which was negatively correlated between midparental inbred lines and derived hybrids ($r = -0.36$, $n = 41$, $p < 0.05$; Fig. 2), and was mostly related to a specific male tester effect. Also in year two, there was

Table 5. Mean parental heterosis (MPH) for optimum stand density (OSD) and yield at OSD (Y_{OSD}).

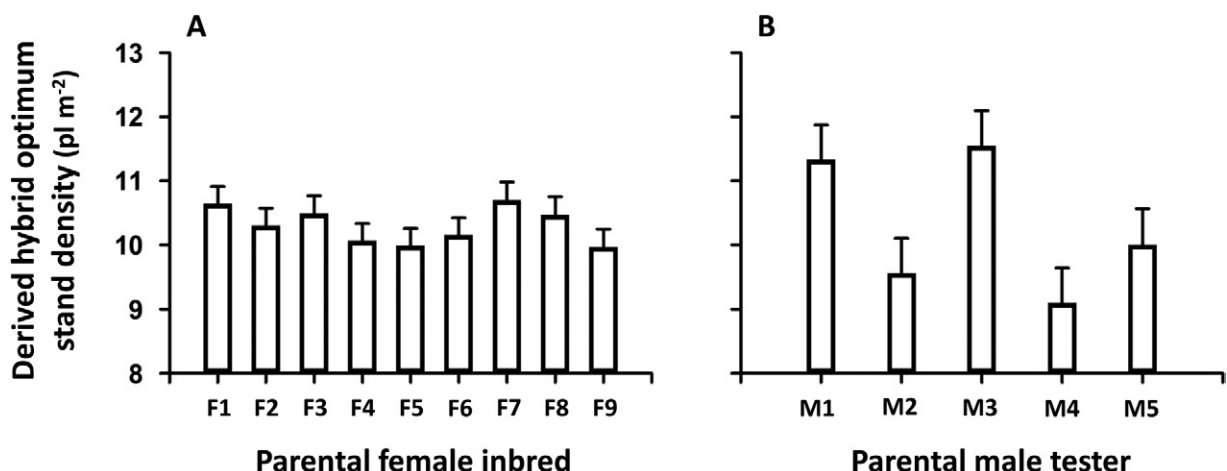| Trait	Mean MPH	Range	Year 1 MPH	Year 2 MPH
			%	
OSD	2	−44–109	−12	16
Y_{OSD}	400	221–1127	330***	470***

*** $p < 0.001$.

Fig. 1. Optimum stand density for derived hybrids, averaged by (A) female inbreds and (B) male testers.
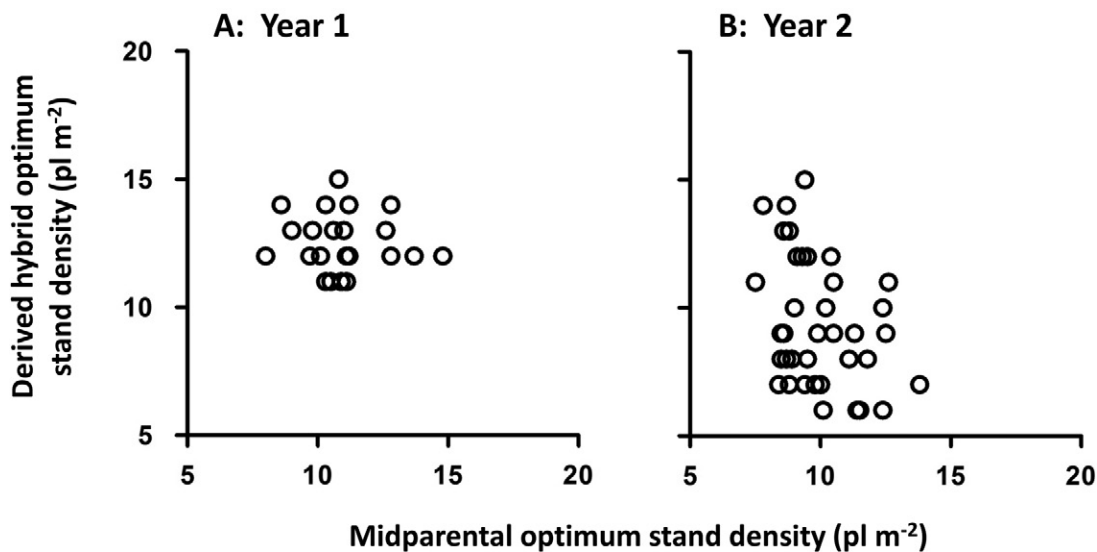
Fig. 2. Correlation between derived hybrid and mean parental inbred line values for optimum stand density at (A) year one and (B) year two ($r = -0.10$, $n = 23$, $p > 0.05$ and $r = -0.36$, $n = 41$, $p < 0.05$ for years one and two, respectively).

a significant and positive correlation between male tester and hybrid performance for yield at OSD ($r = 0.39$, $n = 41$, $p < 0.01$). When data were evaluated altogether, significant correlations were found for yield at OSD ($r = 0.74$, $n = 74$, $p < 0.001$). However, this correlation was driven by environmental differences between years one and two. No evident patterns were observed between inbred lines and derived hybrids responses.

DISCUSSION

Because contrasting stand density responses among current commercial genotypes have been reported (Sarlangue et al., 2007; Tokatlidis et al., 2011; Berzsenyi and Tokatlidis, 2012; Hernández et al., 2014), crop managers are seeking information about genotype × stand density interactions, and seed companies are currently providing genotype-specific recommendations for stand density management. The generation of this information comes with a large effort, in which commercial and precommercial genotypes are tested at a range of stand densities and environments to provide accurate recommendations. In the present study, we tested if inbred line stand density performance could help estimate the derived hybrid stand density performance.

Several experiments have highlighted specific physiological mechanisms behind genotype differences in stand density yield response (Sarlangue et al., 2007; Tollenaar and Lee, 2011; Hernández et al., 2014), and recent studies have started dissecting the genetic basis of these traits using segregating populations (Amelong et al., 2015). At present, we have made no attempt in describing these possible mechanisms, instead wanting to understand the general parental inbred line and derived hybrid correlation for stand density yield response. Unfortunately, derived hybrid OSD performance could not be simply predicted from the midparental inbred line performance. Despite

the lack of correlation between inbred lines and derived hybrids, parental inbred line effects (either female inbred or male tester) on OSD were evident, with no consistent female inbred × male tester interaction effects. As such, parental inbred lines did show a strong effect on the OSD of their derived hybrids (Table 3), generating information of how derived hybrids will perform in relation to stand density management (Fig. 1). Pedigree information, more so than the specific inbred response to stand density, can be considered valuable information for estimating derived hybrid stand density response.

Hernández et al. (2014) evaluated a set of commercial hybrids from Argentina and found genotypic yield differences at higher stand densities, but not at lower ones. That is, evaluated hybrids differed in their tolerance to stress, but not in their potential yield per plant. In the present study, by testing a larger set of inbred lines and derived hybrids, we found significant yield differences not only at the highest stand density but also at the lowest one (Table 2), showing that these genotypes differed in yield potential per plant and in crowding stress tolerance. These differences at low stand density are relevant for developing genotypes with different yield at very low stand densities (Berzsenyi and Tokatlidis, 2012; Tokatlidis, 2013). Hybrid yields at the lowest stand density (1 plant m^{-2}) were correlated to yield at their OSD ($r = 0.25$, $n = 117$, $p < 0.01$ for year one; $r = 0.47$, $n = 118$, $p < 0.001$ for year two), showing that in our study's yield differences were not only related to stress tolerance. Such differences in yield potential per plant can also be exploited in the future for alleviating the strong yield–stand density relationship (Egli, 2015).

We did not find significant differences for OSD between inbred lines and derived hybrids, but only for their yields at this OSD. Yield differences found between

inbred lines and hybrids at similar stand densities were expected (Hallauer et al., 2010). As far as we are aware, this is the first study calculating the OSD that maximizes yield for a set of inbred lines and derived hybrids and shows no significant differences. Although no significant inbred line–derived hybrids correlation was found for OSD, high correlation between yield at the highest stand density and OSD was observed within each type of germplasm ($p < 0.001$, $r = 0.66$, $n = 81$ and $p < 0.01$, $r = 0.52$, $n = 25$ for hybrids and parental lines, respectively). This supports our previous finding that genotypic differences in OSD are driven by genotypic differences in crowding tolerance (Hernández et al., 2014). That is, parental lines and hybrids with higher crowding tolerance supported greater stand densities through smaller decreases in their individual plant yield.

Finally, heterosis, which is the difference between hybrid performance and average parental performance, is an important component of the genetic effect. Our data showed heterosis for yield at similar stand density and for yield at OSD, but not for OSD. Munaro et al. (2011) showed that there is a positive relationship between plant grain yield heterosis and environmental quality until a threshold value, beyond which further increases in environment means did not translate into higher heterosis for plant grain yield. On the contrary, Betrán et al. (2003) showed that differences in grain yield between hybrids and inbreds increased with the intensity of drought stress. Our results show relatively few differences in grain yield heterosis across stand density stress levels (grain yield varied much more than heterosis values, Tables 2 and 4), indicating the possibility of exploiting both yield potential per plant and crowding stress tolerance for increasing yields in future breeding programs.

CONCLUSIONS

A set of inbred lines and derived hybrids was evaluated at contrasting stand densities for testing if hybrid stand density response could be predicted from parental inbred lines response. The hybrids tested showed significant differences in their yield response to stand density, differing in the OSD that maximized their yield.

Correlations between parental inbred lines and derived hybrids were not significant for OSD or yield at different stand densities. We could not predict the OSD of hybrids by calculating their midparental value, but it was evident that specific parental inbreds produced hybrids with higher OSD. As such, the pedigree, more than the specific inbred response to stand density, is relevant information when estimating derived hybrid stand density response.

Conflict of Interest

The authors declare that there is no conflict of interest.

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