



Inter-plant competition for resources in maize crops grown under contrasting nitrogen supply and density: Variability in plant and ear growth

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ABSTRACT

Increased plant population density in irrigated and fertilized maize crops enhances plant-to-plant variability since early vegetative stages, because the most suppressed individuals of the stand intercept less radiation per unit leaf area than the dominant ones (i.e. a size-asymmetric competition for light). Contrarily, a size-symmetric competition has been proposed for the acquisition of soil resources in a plant community (e.g. N capture per unit root length is similar among plants of different size). Hence, N fertilization effect on the variability of maize plants would depend on the initial plant-to-plant variability or on that promoted by a high plant population density. Two maize hybrids with contrasting tolerance to crowding (tolerant AX820 and intolerant AX877) were cultivated under different combinations of stand densities (6, 9 and 12 plants m⁻²) and N supplies (0 and 200 kg N ha⁻¹) without water restrictions. Variability in plant growth rate among plants was computed along the cycle, especially after fertilizer was applied (i.e. the early reproductive period; PGR_{ER}) and during the critical period around silking (PGR_{CP}). Plant-to-plant variability in biomass partitioning to the ear (partition index; PI), ear growth rate during the critical period (EGR_{CP}) and kernel number per plant (KNP) was also established. Reduced N supply increased the coefficient of variation (CV) of PGR_{ER}, PGR_{CP}, EGR_{CP} and KNP (0.05 < P < 0.10). The CVs of PGR_{CP}, PI, EGR_{CP} and KNP augmented (0.001 < P < 0.10) at the highest stand density. The CVs of PGR_{ER}, PGR_{CP}, PI and KNP were larger for hybrid AX877 than for hybrid AX820 (0.001 < P < 0.10). N fertilization smoothed the initial plant-to-plant variability, but the extent of this benefit in a maize crop is genotype dependent; it was much larger in the hybrid tolerant to crowding stress than in the intolerant one. For the latter, the variability held during the critical period around silking and produced a high CV of KNP.

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1. Introduction

Grain yield of maize (*Zea mays* L.) crops is mainly determined by the final number of kernels per unit area that reach maturity. This number is strongly related to crop growth rate during a critical period of 30 days centered at silking and to biomass partitioning to the ear during this period (Andrade et al., 1999). Management practices like stand density (Maddonni et al., 2006) or nitrogen fertilization (Uhart and Andrade, 1995) can affect these physiological attributes and consequently final kernel number.

A per-plant-level analysis (Tollenaar et al., 1992; Vega et al., 2001b) called attention on important physiological traits revealed by the curvilinear response of kernel number per plant (KNP) to plant growth rate (PGR) during the critical period (PGR_{CP}). One outstanding trait was the existence of a minimum PGR_{CP} for avoiding plant barrenness. Another important trait was the PGR_{CP} above

which KNP did not increase (non prolific hybrids, those with no capacity for setting kernels in more than one ear) or started a second phase of increment (prolific hybrids, those capable of setting kernels in more than one ear). The high level of resources per plant experienced at very low stand density caused an increase in PGR_{CP}, up to values for which KNP reaches a plateau or the expression of prolificacy > 1. Contrarily, the minimum or threshold PGR_{CP} corresponded to conditions of reduced resource availability per plant, usually explored under supra optimum stand densities, water deficit, or low soil fertility (Andrade et al., 2002). Interestingly, different plant types (e.g. dominant and dominated) coexist in most commercial maize crops independently of stand density and due to different management problems (e.g. uneven plant distribution; Liu et al., 2004), yielding a wide range of PGR_{CP} (Maddonni and Otegui, 2004).

Grain yield improvement of maize depended upon enhanced tolerance to increased stand density (Duvick, 2005), which reduced the number of barren plants and increased the number of harvestable kernels (Tollenaar, 1989). Research with Argentine hybrids (Echarte et al., 2004; Luque et al., 2006) from different breeding eras

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demonstrated that the modern ones had (i) improved kernel set per unit PGR_{CP} at rates close to the minimum (i.e. high initial slope), and (ii) increased plateau of KNP at high PGR_{CP} (i.e. reduced morphogenetic limitation because of increased spikelet numbers per ear). There is, however, no consensus about breeding effects on the minimum PGR_{CP} for avoiding plant barrenness. Some authors indicated a reduction in this threshold (Echarte et al., 2004), but others found no trend (Tollenaar et al., 1992) or suggested an increase (Luque et al., 2006). Independently of this controversy, all results (*op.cit.* and Echarte et al., 2000) demonstrated that maize breeding promoted an increase in the quotient between KNP and PGR_{CP} , chiefly driven by enhanced biomass partitioning to the ear and not by increased kernel set per unit ear growth rate during the critical period (EGR_{CP}).

High stand densities used in current maize production promote a high level of intra-specific competition, which causes an early increase in interplant variability within the stand. This variability holds during the critical period for kernel set and affects biomass partitioning to the ear (Maddonni and Otegui, 2004; Pagano and Maddonni, 2007). This is the subjacent reason of the tight relationship between PGR before the critical period (i.e. between V_7 and V_{12} ; Ritchie and Hanway, 1982) and PGR_{CP} (Pagano and Maddonni, 2007). This relationship supports the idea of a conditioning effect of early growth stages (plant growth rate during early reproductive growth, PGR_{ER}) on the overall plant performance from the start of the critical period onwards, and the consequent effects on biomass partitioning to the ear and its final reproductive fate (Borrás et al., 2007). Nevertheless, no relationship was found between PGR_{CP} and PGR_{ER} for data obtained under a high irradiance regime (e.g. thinning) established at the start of active stem elongation (from V_9 onwards), because plant compensatory growth took place in the subsequent stage (Pagano and Maddonni, 2007).

Several works described the negative effects of N stress on final kernel numbers (McCullough et al., 1994a,b; Uhart and Andrade, 1995; Boomsma et al., 2009). These negative effects have been related to reductions in PGR_{CP} (Andrade et al., 2002), and biomass partitioning to reproductive organs (D'Andrea et al., 2008). All these studies gave no evidence on the response of interplant variability to reduced N availability and its interaction with contrasting stand densities. In a recent research, Boomsma et al. (2009) reported an increased per plant grain yield variability in response to the combined effect of enhanced stand density and reduced N supply, but did not elucidate the underlying physiological processes of this response. In previous research (Pagano and Maddonni, 2007), we demonstrated that release of light stress by thinning the crop at the start of the early reproductive period, reduced plant to plant variability due to an enhanced growth rate of the most suppressed individuals of the stand. This response, detected in the absence of N deficiency, indicates that competition for light among plants of a crop is *asymmetric* (Casper and Jackson, 1997; Berntson and Wayne, 2000); i.e. light capture per unit leaf area is larger in dominant than in dominated individuals of the stand. Competition for N, in contrast, has been described as *symetric*; i.e. N capture per unit root length does not differ among mentioned plant categories. Consequently, an increase in the availability of resources should allow a differential growth recovery among individuals (e.g. dominated > dominant) in case of a stress that causes an asymmetric response as compared to one that causes a symmetric response. Previous studies (Pagano and Maddonni, 2007) yield evidence for supporting the first part of this hypothesis (i.e. asymmetric recovery) by means of strategic thinning applied on crops growing at above-optimum stand density. Currently, however, there is no evidence for (i) supporting the second part of the analysis (i.e. symmetric recovery), and (ii) the interpretation of responses among plants subjected to combined abiotic stresses (e.g. N and stand density), which are the most common growing condition experienced by

commercial crops. The existence of genotypic variability for the early establishment of plant hierarchies within a stand (Pagano and Maddonni, 2007) is an additional constraint for the correct prediction of responses in these situations. With this purpose we developed field experiments that included two maize hybrids of contrasting stability in grain yield growing under different combinations of stand densities and N supply at the start of active stem elongation. Our objectives were to (i) characterize individual plant growth within each stand, (ii) evaluate the variability in PGR_{ER} , PGR_{CP} , EGR_{CP} , and KNP among plants, and (iii) analyze the relationship between traits listed in (ii).

2. Materials and methods

2.1. Crop husbandry and experimental design

Field experiments were conducted during 2006–2007 (Exp 1) and 2007–2008 (Exp 2) in the Experimental Station of the National Institute of Agricultural Technology (INTA) located at Pergamino (33°56'S, 60°34'W), on a silty clay loam soil. The top soil (0–40 cm layer) had an organic matter content of ca. 23 g kg⁻¹, mean mineral P content of ca. 115 mg kg⁻¹, and inorganic N at sowing of ca. 14 g kg⁻¹. Two hybrids (H) were used, *a priori* classified as contrasting in the stability of grain yield response to increased stand density across environments (Pagano and Maddonni, 2007): low-tolerant Nidera AX877 CL-MG (hereafter AX877) and high-tolerant Nidera AX820 CL-MG (hereafter AX820). Each hybrid was grown at two (Exp 1) or three (Exp 2) stand densities (D_n) and two nitrogen (N_n) levels. Tested stand densities were 6 (D_6 ; only in Exp 2), 9 (D_9) and 12 (D_{12}) plants m⁻². Nitrogen rates were a control with no added N (N_0) and 200 kg of N ha⁻¹ (N_{200}) added as urea at V_6 , because variation in plant growth among plants tends to stabilize at this stage (Maddonni and Otegui, 2004; Pagano and Maddonni, 2007). Treatments were distributed in a split-plot design, with N levels in the main plot and all hybrid × stand density combinations in the sub-plots (herein termed plots). Plots had six rows with an E–W orientation, 0.7 m between rows and 18 m length.

Manual sowing took place on 20-Oct (Exp 1) or 22-Oct (Exp 2) at a rate of 3–4 seeds per hill. Plots were thinned to one plant per hill at the end of the heterotrophic phase (ca. V_3 ; Pommel, 1990). All experiments were kept free of weeds by means of chemical (4 L of atrazine 0.5 a.i. per ha plus 2 L of acetochlor 0.9 a.i. per ha at sowing) and manual controls. Water stress was prevented by means of sprinkler irrigation, with the uppermost soil profile (1 m) near field capacity throughout the crop cycle.

2.2. Phenological events and plant biomass estimation

A total of 10 (Exp 1) or 12 (Exp 2) consecutive plants of similar size (visual assessment) were tagged at V_3 in each plot. Vegetative (V_n) and reproductive (R_n) stages were registered weekly for all tagged plants (Ritchie and Hanway, 1982), including silking (R_1) and anthesis dates. Plant biomass was also estimated weekly between V_3 and $R_1 + 15$ days (R_2) for these plants, by means of allometric models based on nondestructive morphometric measurements.

For each hybrid, 15–20 plants were collected weekly for building mentioned models (Maddonni and Otegui, 2004; Pagano and Maddonni, 2007), based on relationships established between morphometric measurements and plant biomass. Measurements included stem diameter at the base of the stalk (maximum and minimum values), plant height from ground level to the ligule of the last fully expanded leaf, and maximum ear diameter (apical and subapical, when present). Relationships included (i) stem volume and plant biomass (ear excluded at R_2), and (ii) maximum ear

Table 1

Parameters of the allometric models used to estimate: (i) plant biomass (g) during the pre-silking period (V_3 – R_1) and at 15 days after silking (R_2), and (ii) ear biomass (g) at silking (R_1) and at 15 days after silking (R_2). The coefficient of determination (r^2) and the number of data (n) used for model fitting are indicated.

Experiment	Hybrids	Plant biomass estimation						
		V_3 – R_1				R_2		
		a	b	c	r^2, n	d	e	r^2, n
Exp 1	AX820	0.18a	152.2b	0.107a	0.97, 121	22.7b	0.079c	0.95, 100
	AX877	0.18a	138.8b	0.095a	0.97, 134	19.6b	0.088c	0.93, 89
Exp 2	AX820	0.20a	373.8a	0.094a	0.98, 149	32.5a	0.122b	0.88, 90
	AX877	0.19a	647.7a	0.136a	0.96, 171	17.7b	0.177a	0.94, 89
Ear biomass estimation								
R_1 – R_2								
		f		g		r^2, n		
Exp 1 + Exp 2		AX820		0.65a		0.089a		
Exp 1 + Exp 2		AX877		0.60a		0.093a		

Different letters within a column indicate significant differences ($P < 0.05$) between hybrids and experiments.

diameter and ear biomass (R_1 and R_2). Stem volume was obtained from the cylinder formula, using average stalk diameter and stem length for its computation. A bi-linear relationship was set for the pre-silking stage (Eqs. (1) and (2)), and a linear one for R_2 (Eq. (3)). Ear biomass (in g) was estimated by means of an exponential model (Eq. (4)).

$$\text{Plant biomass (g)} = a \text{ Vol}, \quad \text{for } \text{Vol} \leq b \quad (1)$$

$$\text{Plant biomass (g)} = ab + c(\text{Vol} - b), \quad \text{for } \text{Vol} > b \quad (2)$$

$$\text{Plant biomass (g)} = d + e \text{ Vol} \quad (3)$$

$$\text{Ear biomass (g)} = f \exp(gD) \quad (4)$$

where a, b, c, d, e, f and g are model parameters, Vol is stem volume (in cm^3), and D is maximum ear diameter. Model parameters are listed in Table 1.

Morphometric variables were also registered for each tagged plant on each sampling date, and their biomass estimated by means of the described models. All tagged plants were harvested at physiological maturity (R_6) for determination of individual plant biomass. The number of grained ears per plant (i.e. prolificacy) was counted, and a plant was considered barren when it had less than ten grains. Ears were hand shelled and grains were weighed for computing plant grain yield. The number of kernels was counted separately for each apical and subapical ear (when present), and final kernel number obtained for each plant (KNP). Plant biomass evolution (estimated between V_3 and R_2 , and observed at R_6) was represented on a thermal time (TT) basis using a base temperature of 8°C (Ritchie and NeSmith, 1991).

2.3. Data analysis

Growth rates were estimated for each tagged plant from the slope of the linear regression fitted to the evolution of plant (PGR, in g d^{-1}) or apical ear biomass (EGR, in g d^{-1}). The former was evaluated for a sub-period before silking, identified as early reproductive (PGR_{ER}, between V_7 and V_{12}). The latter was computed for the critical period (EGR_{CP}), and was based on three data for each plant: (i) ear biomass = 0 at 227°C d before R_1 (Otegui and Bonhomme, 1998), (ii) estimated ear biomass at R_1 , and (iii) estimated ear biomass at R_2 . Similarly, estimated plant biomass at R_1 – 15 days, R_1 and R_2 were used for computing plant growth rate during the critical period around silking (PGR_{CP}).

Biomass partitioning to the ear (PI: partitioning index) was estimated for each tagged plant as the quotient between EGR_{CP} and PGR_{CP}.

For the whole data set, KNP was related to EGR_{CP} by means of a hyperbolic function (Vega et al., 2001a) of the type described in Eq. (5).

$$\text{KNP} = \frac{h(\text{EGR}_{\text{CP}} - \text{EGR}_{\text{CPT}})}{1 + i(\text{EGR}_{\text{CP}} - \text{EGR}_{\text{CPT}})}, \quad \text{for } \text{EGR}_{\text{CP}} > \text{EGR}_{\text{CPT}} \quad (5)$$

where h is the initial slope, EGR_{CPT} is the threshold ear growth rate for KNP = 0 and i is the degree of curvilinearity at high EGR_{CP}.

The effect of treatments (i.e. N levels and stand densities of 9 and 12 plants m^{-2}) and their interactions were evaluated across years for all described traits by ANOVA. The whole data set (including D_6) was used for testing the relationships among variables by means of TBLCURVE (Jandel, 1992). The coefficient of variation among plants (CV, in %) was computed at a plot level for all traits, and its response to treatments and treatment interactions was also analyzed by ANOVA. A confidence interval of 95% was used for estimating significant differences between hybrids in the parameters of the hyperbolic function.

3. Results

3.1. Plant biomass

No difference was detected between years, but reduced N supply caused a decrease in mean plant biomass (Fig. 1a), which was significant ($P < 0.01$) from V_8 onwards. This trend caused a decrease of ca. 40% in final plant biomass (R_6) for N_0 . Plant biomass reduction in response to increased stand density started at V_{12} ($P < 0.05$). The reduction in final plant biomass (R_6) when stand density was increased from D_9 to D_{12} was 19% (Fig. 1b). Nitrogen $\times$ density interaction ($P < 0.05$) was detected for plant biomass at R_2 and R_6 , when D_9 was greater than D_{12} in N_{200} , while no differences were detected between densities in non fertilized plots (data not shown). Hybrids exhibited similar plant biomass along the cycle.

The CV of plant biomass decreased from V_3 (starting values of 36%) to V_8 (Fig. 1c and d), when it stabilized at low values (27%). The CV of plant biomass was markedly affected by N supply, when the differences between N treatments were detected from V_8 onwards (Fig. 1c). Contrarily, stand density did not modify this trait (Fig. 1d).

A significant N $\times$ hybrid $\times$ stand density interaction was detected for the CV of plant biomass at R_2 and R_6 ($P < 0.05$). At R_2 , differences in this trait between N levels were observed only for hybrid AX877 at D_{12} . For this hybrid, significant differences were detected between stand densities only at N_0 (CV of 24 and 32% for D_9 and D_{12} , respectively). This trend held at R_6 for hybrid AX877, but differences were significant only between N levels at D_{12} (data

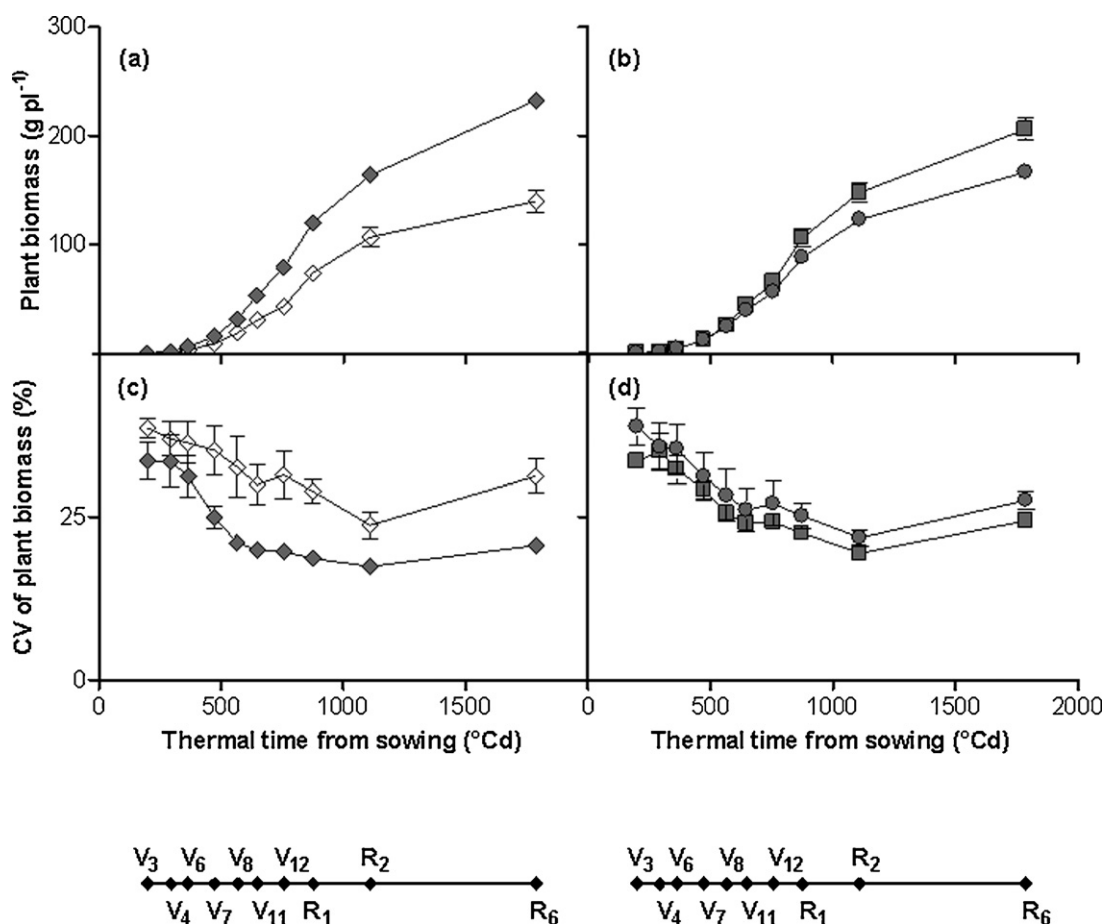


Fig. 1. Plant biomass evolution (a and b) and CV of plant biomass (c and d) of hybrids AX820 and AX877 during both experiments. Empty and full diamonds are for N_0 (no N added) and N_{200} (fertilized with 200 kg N ha^{-1}), respectively. Squares and circles are for 9, and 12 plants m^{-2} , respectively. Ontogenic stages of crops are detailed at the bottom of each figure.

not shown). At this stage, differences between N levels were also detected for hybrid AX820, but were significant at D_9 rather than at D_{12} .

3.2. Plant growth rate, biomass partition around silking, ear growth rate and kernel number

In both growing seasons, low N supply and increased stand density reduced PGR_{ER} , PGR_{CP} , EGR_{CP} and KNP (Table 2). Hybrids had similar PGRs for all periods under analysis (early reproductive and critical), but a significant Experiment (E) $\times$ H interaction indicated that (i) PGR_{ER} was larger in Exp 1 than in Exp 2 for AX877, and (ii) PGR_{CP} was larger in Exp 1 than in Exp 2 for AX820. A slight ($P < 0.10$) $N \times$ stand density effect was detected for PGR_{ER} and PGR_{CP} , which pointed out a negative effect of increased stand density at high N supply.

A positive and significant ($P < 0.001$) relationship was detected between PGR_{CP} and PGR_{ER} ($r^2 = 0.68$) for the whole data set. This relationship held ($P < 0.001$) across treatments. For AX820 (Fig. 2a), r^2 values were larger for low ($\text{PGR}_{\text{CP}} = 0.51 + 1.07 \text{ PGR}_{\text{ER}}$, $r^2 = 0.68$; $P < 0.001$) than for high N supply ($\text{PGR}_{\text{CP}} = 0.34 + 1.11 \text{ PGR}_{\text{ER}}$, $r^2 = 0.34$; $P < 0.001$). Although this trend was similar for AX877 (Fig. 2b), r^2 values were always higher ($\text{PGR}_{\text{CP}} = 0.65 + 0.9 \text{ PGR}_{\text{ER}}$, $r^2 = 0.82$; $P < 0.001$ at N_0 and $\text{PGR}_{\text{CP}} = 1.22 + 0.74 \text{ PGR}_{\text{ER}}$, $r^2 = 0.63$; $P < 0.001$ at N_{200}) than for AX820.

Biomass partition to the ear around the critical period (i.e. PI) was not affected by reduced N supply and increased stand density, but differed between hybrids (Table 2 and Fig. 2c and

d). Hence, a significant relationship ($P < 0.001$) was established between EGR_{CP} and PGR_{CP} across experiments for each hybrid ($r^2 = 0.90$ for AX820, $r^2 = 0.80$ for AX877). Hybrid AX877 had always the lowest EGR_{CP} due to the smallest PI. Final KNP, however, did not differ between hybrids (Table 2). No barren plant was registered for AX820. Contrarily, 5% of barren plants (17 plants with less than 10 kernels) were detected for AX877. For both hybrids, plants with more than 1 ear were never detected at D_9 and D_{12} .

Plant-to-plant variability of several traits was affected by treatments (Table 2). Reduced N supply increased the CV of PGR_{ER} , PGR_{CP} , EGR_{CP} and KNP ($0.05 < P < 0.10$). At the highest stand density the CVs of PGR_{CP} , PI, EGR_{CP} and KNP was augmented ($0.001 < P < 0.10$) (Table 2). The CV of PGR_{ER} , PGR_{CP} , PI and KNP were larger for hybrid AX877 than for hybrid AX820 ($0.001 < P < 0.10$). A significant $N \times H \times$ stand density was detected for the CV of EGR_{CP} ($P < 0.01$) and KNP ($P < 0.10$). Reduced N supply only caused an increase in CV of EGR_{CP} for hybrid AX877 at D_{12} . The CV of KNP augmented in N stressed plots of AX877 growing at D_9 and D_{12} , and only at D_9 for AX820.

3.3. KNP response to EGR_{CP}

The variation in KNP was explained by the variation registered in EGR_{CP} by means of a curvilinear function ($r^2 \geq 0.70$, Table 3 and Fig. 2e and f), which capture plant-to-plant variability across treatments and experiments. A single function was fitted for AX820 data set because parameters of the function were not affected by

Table 2
Plant growth rate during the early reproductive period (PGR_{ER}), and the critical period (PGR_{CP}), ear growth rate during the critical period (EGR_{CP}), partitioning index (PI), kernel number per plant (KNP) and their coefficients of variation (CV) of two hybrids (H) cultivated at two plant population densities (D) and two N levels (N₀: unfertilized; N₂₀₀: fertilized). Values are the mean of two growing seasons (Exp 1 and Exp 2; E).

Hybrid	Density pl m ⁻²	Nitrogen	PGR _{ER} g d ⁻¹	PGR _{CP} g d ⁻¹	EGR _{CP} g d ⁻¹	PI	KNP	CV (%)				
								PGR _{ER}	PGR _{CP}	EGR _{CP}	PI	KNP
AX820	9	0	1.75	2.56	1.09	0.35	335	26.9	20.4	31.8	13.9	25.4
		200	3.16	4.05	1.78	0.39	499	15.5	17.3	23.6	12.3	13.4
	12	0	1.56	2.21	0.90	0.35	310	32.1	23.5	36.4	15.9	28.4
		200	2.69	3.08	1.32	0.38	418	18.8	23.4	36.7	22.3	22.4
AX877	9	0	1.82	2.40	0.78	0.31	359	29.0	27.7	32.4	17.1	38.4
		200	3.75	4.20	1.34	0.30	534	25.6	24.8	29.3	19.0	26.1
	12	0	1.61	2.03	0.63	0.29	276	37.2	34.4	47.1	25.8	64.7
		200	2.82	3.02	0.97	0.30	446	19.2	22.5	28.5	22.5	25.3
Significance level of main and interaction effects												
	E					*						
	N		**	**	*		**	*	†	*		*
	H				**	***		†	**		†	***
	D		**	***	**		**		†	***	*	*
	E × N										†	
	E × H		†	**	**	***						
	N × H									†		†
	H × D											
	E × D											
	N × D		†	†								
	E × N × H					*						
	E × N × D											†
	E × H × D											
	N × H × D									**		†
	E × N × H × D											

† Significance level at $P < 0.1$.

* Significance level at $P < 0.05$.

** Significance level at $P < 0.01$.

*** Significance level at $P < 0.001$.

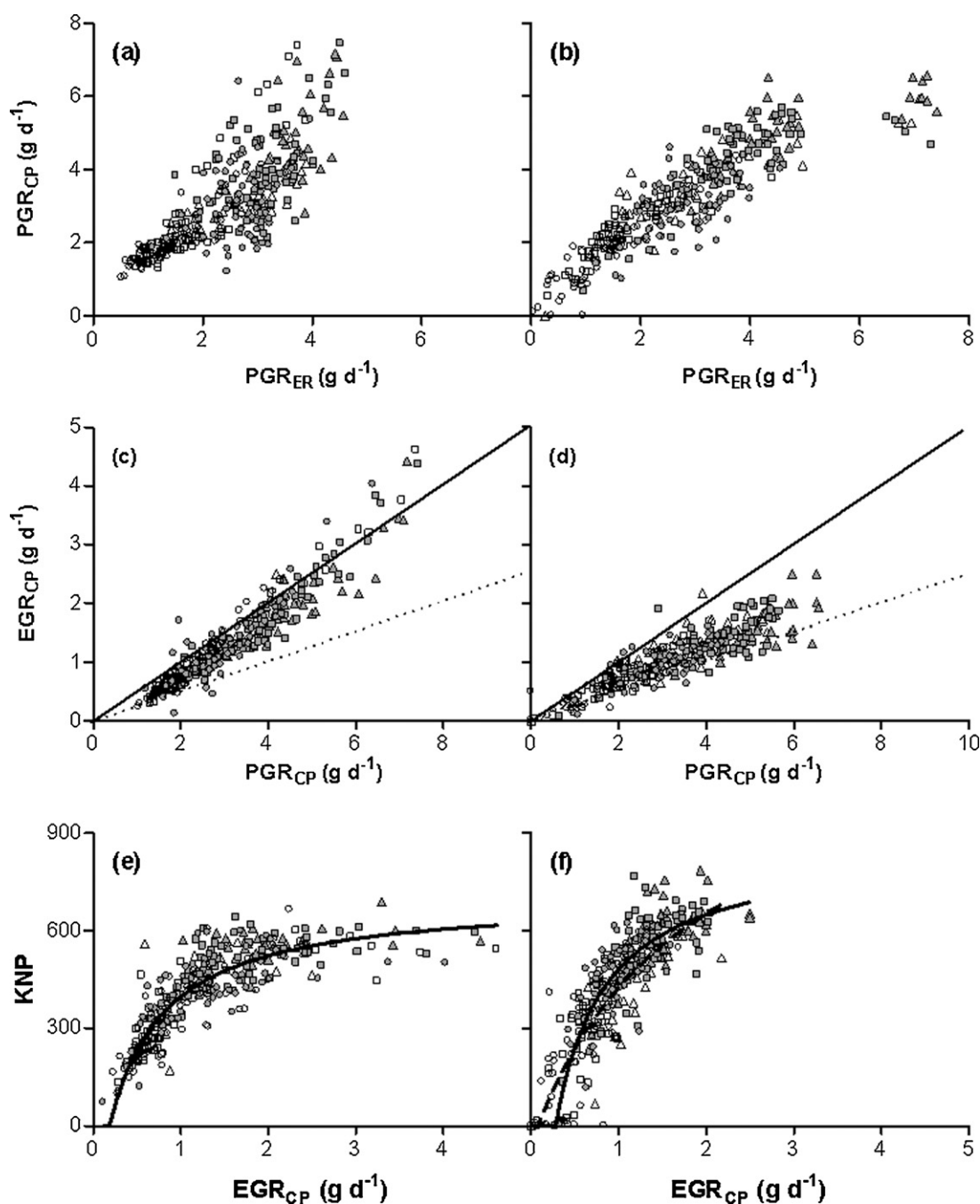


Fig. 2. Relationships between plant growth rates (PGR) obtained at early reproductive (PGR_{ER} , between V_7 and V_{12}) and critical (PGR_{CP} , between $R_1 - 15$ d and R_2) periods (a and b), ear (EGR_{CP}) and plant (PGR_{CP}) growth rates during the critical period (c and d), and response of kernel number per plant (KNP) to EGR_{CP} (d and e) of hybrids AX820 (a, c and e) and AX877 (b, d and f). Data correspond to hybrids AX820 and AX877 grown at N_0 (empty symbols) and N_{200} (full symbols). Symbols: triangles (6 plants m^{-2}); squares (9 plants m^{-2}); and circles (12 plants m^{-2}). The lines in (c) and (d) represent the 0.50 (solid) and 0.25 (dotted) ratios between EGR_{CP} and PGR_{CP} (i.e. biomass partitioning to the ear). For AX820 in (e): $KNP = 1123 (EGR_{CP} - 0.19) / (1 + 1.6 (EGR_{CP} - 0.19))$ for $EGR_{CP} > 0.19$ ($r^2 = 0.76$, $n = 334$; $P < 0.01$). For AX877 N_0 (dotted line) in (f): $KNP = 680.4 (EGR_{CP} - 0.07) / (1 + 0.52 (EGR_{CP} - 0.07))$ for $EGR_{CP} > 0.07$ ($r^2 = 0.70$, $n = 167$; $P < 0.01$); for AX877 N_{200} (full line) in (f): $KNP = 1513 (EGR_{CP} - 0.28) / (1 + 1.7 (EGR_{CP} - 0.28))$ for $EGR_{CP} > 0.28$ ($r^2 = 0.70$, $n = 168$; $P < 0.01$).

treatments. Contrarily, for AX877 the threshold EGR_{CP} for $KNP=0$ ($EGR_{CP,T}$), the initial slope (h) and the curvature (i) were larger for N_{200} than for N_0 .

Differences between hybrids held for the relationship between the CVs of these traits. Increased variability in EGR_{CP} promoted by enhanced abiotic stress caused a larger increased in KNP variability of hybrid AX877 ($CV \text{ KNP} = -23.18 + 1.75 \text{ CV } EGR_{CP}$, $r^2 = 0.51$, $P < 0.001$) than of hybrid AX820 ($CV \text{ KNP} = 6.01 + 0.45 \text{ CV } EGR_{CP}$, $r^2 = 0.19$, $P < 0.01$).

4. Discussion

In the current research we studied the responses of maize plants to different stand densities (optimum and supra-optimum plant populations) and contrasting N supplies (fertilized and non fertilized plots), using two commercial hybrids of similar breeding era but distinct tolerance to crowding. Plant responses were evaluated from the start of the autotrophic phase at V_3 (Pommel, 1990) until final harvest at R_6 , and focused at the individual plant level (i.e.

Table 3

Parameters of models fitted to the data set of kernel number per plant (KNP) in terms of EGR_{CP} . Attached is the coefficient of determination (r^2), the values of model parameters and the number of plants used for the adjustment of each model.

Hybrid	Nitrogen	KNP vs. EGR_{CP}			
		Model parameters			
		h (g g ⁻¹ d ⁻¹)	EGR_{CP} (g pl ⁻¹ d ⁻¹)	i (g g ⁻¹ d ⁻¹)	r^2 , n
AX820	$N_0 + N_{200}$	1123a	0.19a	1.60a	0.76, 334
AX877	N_0	680.4b	0.07b	0.52b	0.70, 167
	N_{200}	1513a	0.28a	1.70a	0.70, 168

Different letters within a column indicate significant differences ($P < 0.05$) among treatments.

data representing the population variability). In our experiments, N and stand density stresses caused the expected reduction in plant biomass (Maddonni and Otegui, 2004; Pagano and Maddonni, 2007; Boomsma et al., 2009), but we established that its response to N deficiency preceded (onset at V_8) the response observed to reduced irradiance per plant (onset at V_{12}). The early effect of N stress on plant biomass production, derived from decreased plant leaf area (McCullough et al., 1994a,b; Uhart and Andrade, 1995; Boomsma et al., 2009) and light interception (Jones and Kiniry, 1986; Gallo et al., 1993), indicated that this restriction anticipated the negative effects on these traits caused by enhanced mutual shading due to increased stand density (Kiniry and Knievel, 1995; Pagano and Maddonni, 2007). Nevertheless, more contrasting stand densities (e.g. sub-optimum vs. supra-optimum plant populations; Maddonni et al., 2001) combined with less intense N deficiency (Uhart and Andrade, 1995) could reverse this response.

Temporal analysis of plant-to-plant variability, quantified in the CV of plant biomass (Edmeades and Daynard, 1979), revealed that the natural variability at the start of crop cycle was slightly larger than in previous studies (Maddonni and Otegui, 2004; Pagano and Maddonni, 2007). This condition was probably due to an uneven distribution of the initially low soil N level of the whole experimental site. Persistently high CV values computed for N_0 plots before the start of competition for light due to mutual shading (i.e. leaf area index < 1 ; Smith, 1986) support the hypothesis of 'symmetric' assigned to the acquisition of soil resources, because growth of plants exposed to patches of low N was much reduced than growth of those exposed to patches of high N. Fertilization at V_6 , caused an increase in plant biomass (Boomsma et al., 2009), but also a steeper decline in the CV of this trait as compared to the unfertilized plots. This response clearly revealed the capacity of improved N supply for smoothing the initial variation among plants, which may turn into superior grain yields per unit land area (Tollenaar and Wu, 1999). After fertilization, the drastic reduction in interplant variability indicates that early in the cycle dominated individuals are not permanently affected in their capacity for capturing resources and recovering growth, and that this plant type would be responsible for the homogenization of growth among individuals along the cycle (Vega and Sadras, 2003). This result additionally suggests that the capacity of plants to acquire soil resources may be a dynamic trait and not a constitutive one, strongly depending on the stage of the cycle when the shift in resource availability takes place (Kira et al., 1953). The experimental approach to test these hypotheses should grant (i) a homogenous resource offer, especially at low resource levels (e.g. comparable to that obtain by means of shading for the case of light), and (ii) the evaluation of possible differences in soil resource acquisition between dominant and dominated plants due to an interference of their root systems. This approach does not seem feasible at the field-crop level, except by means of extremely drastic soil (Uhart and Andrade, 1995) and plant manipulations (e.g. split root systems; Satorre and Snaydon, 1992).

An enhanced biomass partitioning to aerial organs (i.e. increased shoot/root ratio) has been reported as an early response of maize plants to the presence of neighbor individuals (Kasperbauer and

Karlen, 1994), and genotypic differences in shoot elongation in response to neighbors has been documented for maize hybrids (Maddonni et al., 2002). This penalty in assimilates allocation to roots may limit the competitive capacity for capturing soil resources (Rajcan and Swanton, 2001). In this context, a larger variation in plant growth should be expected among individuals of unfertilized plots than among their fertilized counterparts, especially in hybrids more reactive to the presence of neighbors. Based on this reasoning, late effects on plant growth (summarized in PGR_{CP}) of environmental conditions experienced early in the cycle (summarized in PGR_{ER}) should be stronger under low than under high N supply. This trend was clearly observed in our research for the tight relationship between PGR_{CP} and PGR_{ER} of the intolerant hybrid. A result that reinforced previous findings from thinning treatments imposed at the start of the early reproductive period (Pagano and Maddonni, 2007), which decreased plant-to-plant variability of the intolerant hybrid and increased PGR_{CP} , with the concomitant reduction in the relationship between PGR_{CP} and PGR_{ER} . Collectively, former (Pagano and Maddonni, 2007) and current findings support the idea of different population performance in response to limiting light and soil resources between canopies of tolerant and intolerant hybrids. Interestingly, results from different intolerant hybrids included in our studies fulfil the concept of a size-asymmetric competition of leaves for light and a size-symmetric competition of roots for nutrients, since late thinning decreased the early variability among individuals, while late N fertilization did not completely modify the initial plant-to-plant variability. By contrast, thinning did not alter the initial low population variability of the tolerant hybrid, but fertilization at the start of the early reproductive period disengaged the relationship between PGR_{CP} and PGR_{ER} . Hence, the intolerant hybrid exhibited a pattern of resource acquisition close to that of a community of different species, where root competition indirectly affects the overall competition among individuals due to root-shoot competition interactions (Lamb et al., 2009). Increasing the intensity of root competition (e.g. environments with low soil fertility) should increase the size-asymmetric competition for light; hence, plant-to-plant variability at early growth stages would influence the final reproductive performance of the stand.

The relationships between PGR_{CP} and PGR_{ER} , EGR_{CP} and PGR_{CP} and between the CV of EGR_{CP} and the CV of KNP of the intolerant hybrid illustrate the early growth effect on reproductive fate. Above-optimum stand density and N deficiency did not uncouple vegetative and reproductive growth (i.e. the biomass partition index estimated from the relationship between EGR_{CP} and PGR_{CP}), as previously reported for some specific genotype $\times$ stand density (Pagano and Maddonni, 2007) or genotype $\times$ N (D'Andrea et al., 2006, 2008) combinations. Biomass partition index, however, was smaller and more variable for the intolerant hybrid AX877 than for the tolerant AX820. This index represents the strength of the ear as a sink for assimilates around flowering, and differences in this trait between hybrids support their distinction as 'stable' (AX820) or 'unstable' (AX877) in grain yield response across environments of contrasting intra-specific competition (Echarte et al., 2004; Luque

et al., 2006; Pagano and Maddonni 2007). Use of EGR_{CP} , however, did not improve the predictive capacity of PGR_{PC} for the estimation of KNP (data not showed) in disagreement with evidences from previous research (Pagano and Maddonni, 2007; D'Andrea et al., 2008). Discrepancies may be related to mentioned genotype-dependent responses, which may affect biomass allocation to the ear but also kernel set per unit ear biomass (D'Andrea et al., 2006, 2008). For the tolerant hybrid, the response of KNP to EGR_{CP} held independently of the factor that was limiting plant growth (N, stand density). Contrarily, for the intolerant hybrid, N stress not only affected EGR_{CP} but also the reproductive efficiency (i.e. kernel set per unit of EGR_{CP}) estimated by the initial slope of the function fitted to KNP and EGR_{CP} data sets. The negative effect of reduced plant growth on kernel set was enhanced by N deficiency (D'Andrea et al., 2008).

5. Conclusions

This work clearly showed the capacity of improved N supply for smoothing the initial variation among plants of maize hybrids with different tolerance to crowding. N fertilization reduced the initial plant-to-plant variability of the tolerant hybrid (AX820). In contrast, N fertilization did not completely modify the initial plant-to-plant variability of the intolerant hybrid (AX877). The close relationship between PGR_{CP} and PGR_{ER} of AX877, even at high N supply, suggests a symmetrical competition for soil resources. Additionally, N stress not only affected EGR_{CP} but also the reproductive efficiency (i.e. KNP per unit of EGR_{CP}) of AX877. This effect was clearly demonstrated by the positive relationship between the CVs of EGR_{CP} and of KNP.

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