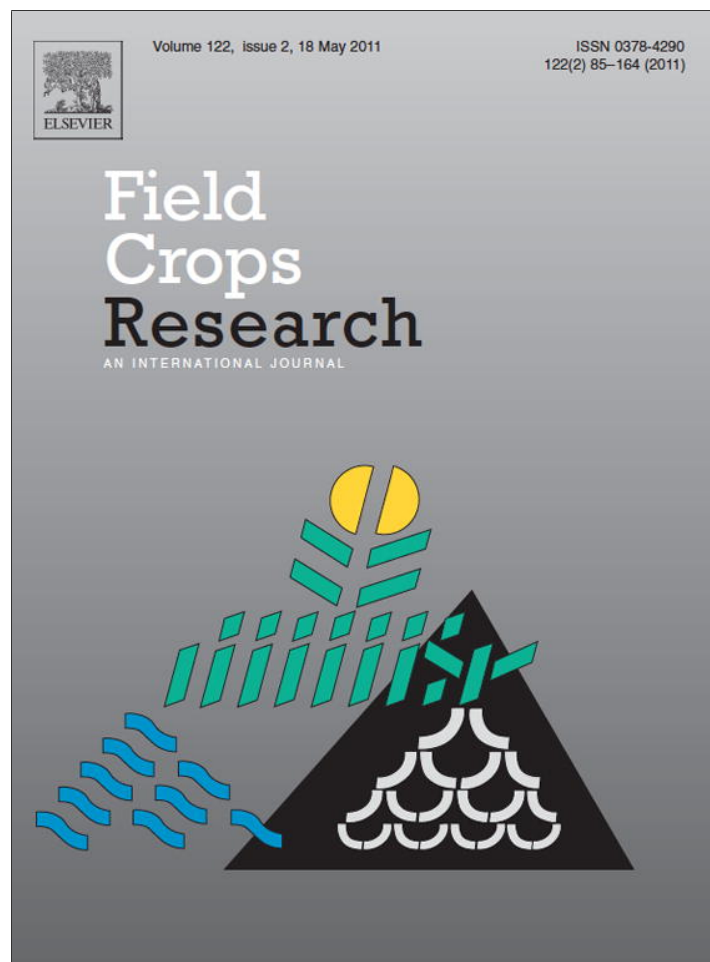


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Contribution of contrasting plant hierarchies to the response to N fertilizer in maize

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ARTICLE INFO

Article history:

Received 16 November 2010

Received in revised form 16 March 2011

Accepted 17 March 2011

Keywords:

Plant hierarchies

Maize

Nitrogen

Intra-specific competition

ABSTRACT

The typical size structuring process that occurs as a consequence of intra-specific competition in maize promotes the appearance of contrasting plant hierarchies (i.e. dominated and dominant individuals). This process may become more intense under low nitrogen (N) availability. The alleviation of plant competition by N addition may reduce plant yield variability through a differential response to N in individuals of contrasting hierarchies. In this work, the response to N of dominated and dominant plants from stands with contrasting N supply (0 to 140–200 kg N ha⁻¹) was examined on 11 experiments carried out in Paraná, Argentina (31°50'S; 60°31'W) in a broad range of growing conditions that included the variation of the year, genotype, plant population and sowing date. Our objectives were: (i) to evaluate the response to N in contrasting plant hierarchies of maize, (ii) to quantify the contribution of dominated and dominant plants to the response to N of the overall stand, and (iii) to study the effect of N on relationships between plant hierarchies and stand variability. Response to N of yield per plant was associated with biomass per plant in non-fertilized controls, tending to be higher in plants with low biomass. The response to N of yield per unit area (i.e., considering all individuals of the stand) was related to the response to N of dominant and dominated plants ($P < 0.0001$). However, at a higher level of response to N of grain yield per unit area (>50–60%), dominant plants had a considerable lower response than dominated plants, whereas at a lower level of response (<30%), the contribution of contrasting plant hierarchies was similar. In stands with similar plant biomass between hierarchies, the differences in the response to N between plant types tended to be negligible. The coefficient of variation of yield per plant was reduced ($P < 0.05$) by effect of N in 4 out of 11 experiments, although it tended to be consistently lower in fertilized treatments. When the differences between the biomass of dominated and dominant plants were ample we found the highest response to N at the stand level, as a result of the higher increase in grain yield per plant in dominated plants than in dominant ones. The response to N in each plant hierarchy was differentially associated with increases in shoot biomass, harvest index, kernel number per plant and kernel weight.

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1. Introduction

The current knowledge on the mechanism of maize yield determination has been gained through successive approaches at different organization levels, in a typical top-down approach, from the canopy to the plant level. At the crop level, kernel yield is

directly related to the crop growth rate during the 30-day period around silking (Tollenaar, 1977; Kiniry and Ritchie, 1985; Otegui and Andrade, 2000), which is the most critical period for yield determination. The crop growth rate, in turn, is associated with the interception of solar radiation and its use efficiency (Uhart and Andrade, 1995), i.e. the growing conditions during the critical period.

At the plant level, yield is also associated with the growing conditions around silking (Andrade et al., 1999). In fact, kernel number per plant (KN_p) shows a curvilinear response relationship with plant growth rate (PGR) during the critical period (Tollenaar et al., 1992; Andrade et al., 1999).

Other studies at the plant level have also been valuable to understand the key role of the growing conditions during the critical period on potential kernel weight determination (Gambín et al., 2006). Several studies have supported these findings using geno-

Abbreviations: d, dominated plants; D, dominant plants; B_p, biomass per plant; CV, coefficient of variation; KN_p, kernel number per plant; PGR, plant growth rate during the critical period; HI, harvest index; KW, kernel weight; MD, mean distance between a plant and its contiguous neighbors in the row; B_p d/B_p D ratio, ratio between B_p of dominated (d) and dominant (D) plants.

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types (Echarte and Andrade, 2006; Gambín et al., 2008), plant population (Gambín et al., 2007) and nitrogen (N) (Melchiori and Caviglia, 2008) as sources of variation in PGR.

Recent research has focused on the determination of maize plant yield in individuals of contrasting hierarchies within a plant population (Maddonni and Otegui, 2004; Boomsma and Vyn, 2009; Boomsma et al., 2009). The results indicate that the response of KN_p to PGR is different between large individuals with an improved performance for competition (dominant plants) and small individuals with less ability to capture and use the environmental resources (dominated plants). In fact, at equivalent PGR values, dominated plants set fewer kernels than dominant plants (Maddonni and Otegui, 2004).

Differences between extreme plant hierarchies have also been reported in dry matter partitioning to the ear (Pagano and Maddonni, 2007), kernel composition and numerical yield components (Maddonni and Otegui, 2006), and flowering dynamics (Pagano et al., 2007).

The establishment of plant hierarchies within a maize plant population has been attributed to several factors such as variability in spatial distribution, time to emergence and seed size (Andrade and Abbate, 2005). However, the early establishment (at V4–V7) of plant hierarchies has also been reported in evenly distributed stands with no evident differences in seedling size and crop emergence (Maddonni and Otegui, 2004). Therefore, the development of hierarchies in maize plant populations seems to be an expected consequence of a size structuring process driven by intra-specific competition.

Three main effects from intra-specific competition are anticipated: (i) a decrease in mean plant size as plant population increases, (ii) an establishment of size hierarchies, and (iii) plant population-dependent mortality (self-thinning) (Park et al., 2003). This last effect is rarely expected in agronomic situations owing to the improbability to reach the combinations of plant size and plant population conducive to mortality of individuals (Enquist et al., 1998; Park et al., 2003).

Most of the studies on intra-specific competition in maize have been conducted under a good supply of nutrients, using plant population (Glenn and Daynard, 1974; Maddonni and Otegui, 2004; Pagano and Maddonni, 2007; Boomsma et al., 2009) and uneven spatio-temporal variability (Liu et al., 2004a; Tollenaar et al., 2006; Andrade and Abbate, 2005) to generate a variable competition intensity, and exposing the plants to a wide range of growing conditions during the critical period.

Plant-to-plant variability, as a result of intra-specific competition in maize, becomes more intense as a result of an increased plant population in a given genotype (Glenn and Daynard, 1974; Maddonni and Otegui, 2004; Andrade and Abbate, 2005; Boomsma et al., 2009). In turn, stand variability leads to a yield reduction both at the crop level (Glenn and Daynard, 1974) and at the plant level (Andrade and Abbate, 2005).

Effects of uneven emergence (temporal variability) and spatial variability on maize yield at the crop level have been widely studied (e.g. Nafziger et al., 1991; Liu et al., 2004a; Andrade and Abbate, 2005; Martin et al., 2005); however, results have been contradictory.

In a review, Tollenaar et al. (2006) concluded that moderate plant-spacing variability does not affect maize grain yield at the crop level, because the yield reduction in crowded plants is compensated by the yield of the plants that experienced reduced crowding stress. In contrast, they reported a reduction in crop yield when plant-to-plant variability increases due to emergence delay, which is associated with a lower harvest index (i.e. "resource utilization") in crowded plants.

Despite the considerable progress that has been made in the knowledge of the mechanisms involved in the intra-specific com-

petition in maize, the plant yield response to N in contrasting hierarchies has been scarcely explored (Boomsma and Vyn, 2009). Although N supply could alleviate the effect of the competition by reducing plant yield variability under low N availability (Boomsma et al., 2009), there are no studies regarding the effect of N on yield, yield component or yield response in individuals of contrasting hierarchies in maize.

The effect of N on the alleviation of competition can not be directly assumed from the results obtained by manipulating plant population, since competition among individuals within the stand can be different depending on the nature of the limiting resource (Park et al., 2003; Weiner, 1990; Casper and Jackson, 1997). Thus, competition for light is predominantly asymmetric, i.e. few dominant individuals use a disproportionately large share of the available resource to the detriment of the growth of dominated individuals (Weiner, 1990), whereas competition for underground resources (e.g. soil nitrogen) has been suggested to be symmetric (Casper and Jackson, 1997).

At the crop level, response to N has been more associated with increases in radiation interception than with changes in its use efficiency, whereas at the plant level, shortage of resources such as water and nitrogen does not change the response of KN_p to PGR (Andrade et al., 2002). In contrast, recent studies have reported that the response of KN_p to PGR as affected by N may be different depending on the genotype and the season (D'Andrea et al., 2006, 2008), thus suggesting that the conclusions obtained through manipulations in plant density are not always applicable to other sources of variation that cause plant growth reduction.

Harvest index (HI) may increase when N availability is increased or improved under limiting conditions (Ciampitti and Vyn, 2011), due to the curvilinear relationship between plant biomass and HI (Echarte and Andrade, 2003). It is therefore expectable that HI increases as N supply increases, up to a threshold where a maximum HI is reached. Although it has been documented that intra-specific competition may affect the biomass and HI (Tollenaar et al., 2006; Pagano and Maddonni, 2007; Boomsma et al., 2009), it is still surprisingly unclear how N may affect the competition and the ability of plant hierarchies to produce biomass and partitioning to the ear, taking into account that N is a key issue in the vast majority of the maize production regions.

The stand response to N may be related to the increase in yield of dominant and/or dominated plants, since plant hierarchies could be differentially responsive to N. Plant yield variability could be lower under high N supply in contrast to controls, if the yield of dominated plants is improved to a greater extent than that of dominant ones.

In this work, the response to N of each plant from stands cropped with contrasting N supply was examined in eleven experiments carried out at a broad range of growing conditions during six cropping seasons that included variation of year, genotype, plant population and sowing date. Our aims were: (i) to evaluate the response to N in contrasting hierarchies of maize plants, (ii) to quantify the contribution of dominated and dominant plants to the response to N of the overall stand, and (iii) to study the effect of N on relationships between hierarchies and stand variability.

2. Materials and methods

2.1. Experiments, crops and management

Eleven field experiments were carried out at INTA experimental station in Paraná, Argentina (31°50'S; 60°31'W; 110 m.a.s.l.) from the 2002/03 to the 2007/08 maize growing season (Table 1).

The maize growing season in our region is characterized by temperate to high average temperatures (20.7 °C from September to

Table 1

Background information for eleven experiments carried out in Paraná, Argentina from 2002/03 to 2007/08 cropping seasons.

Experiment	Season	Hybrid	Planting date	N rate (kg N ha ⁻¹)	Plant population ^a (plant m ⁻²)	Mean yield (kg ha ⁻¹)
1	2002/03	DK682	10 September	0, 140	8.3	7009
2	2002/03	DK682	26 December	0, 50, 200	8.2	7802
3	2002/03	DK752	26 December	0, 140	4.7 and 8.7	7175
4	2002/03	DK682	26 December	0, 140	8.3	7057
5	2003/04	DK682	15 September	0, 140	9.4	9839
6	2004/05	DK682	1 September	0, 140	8.7	9473
7	2005/06	DK747	3 September	0, 140	9.3	4375
8	2006/07	DK684	19 September	0, 140	8.4	10717
9	2007/08	DK684	24 September	0, 140	9.1	6674
10	2007/08	DK684	24 September	0, 140	4.4 and 10.1	6234
11	2007/08	AW190	10 January	0, 140	4.9 and 11.9	8501

^a Average at physiological maturity.

April, ranging from 15.2 to 24.8 °C) and a frost free period of ca. 240 d.

The soil was a fine, mixed, thermic Aquic Argiudoll under no-till since 1998. Organic matter contents in the top 0.25 m were 2.90–3.05%. The soil showed no physical restriction and an adequate P availability (>20 mg kg⁻¹ P Bray). Irrespective of P availability, plots were fertilized with 20 kg P ha⁻¹ as triple super-phosphate at planting.

Relative maturity of maize hybrids (Table 1) ranged from 118–119 (DK682, DK684, AW190) to 124–125 (DK747 DK752).

Experiments 2–5, 8 and 9 were supplementary, sprinkler irrigated. All experiments were kept free of weeds, diseases and insects. In all experiments the previous crop was soybean.

Fertilization treatments (0–200 kg N ha⁻¹) were laid out in a randomized complete block design with 3–4 replicates. Experiments (Exps.) 3, 10 and 11 included a factorial combination of plant population (4.4–4.9 to 8.7–11.9 plant m⁻² at harvest) and N rate. Plots were over-seeded and thinned by hand at V2 stage to reach the final plant population.

Nitrogen was broadcast-applied as urea (46% N) immediately after planting. All experiments were sown with a pneumatic planter. Plant population was adjusted by thinning at V2 stage. Plots had five rows and were 20 m long. Row spacing was 0.53 m in Exps. 5–11 and 0.70 m in Exps. 1–4.

Normal planting dates (Exps. 1, 5–10) ranged from 1 September to 24 September, whereas late planting dates ranged from 26 December to 10 January (Exps. 2–4 and 11).

2.2. Measurements

Fifteen (Exps. 8–11) or twenty (Exps. 1–7) consecutive plants per plot in the central row were tagged and cut at physiological maturity. The plants were oven-dried until constant weight at 80 °C to determine shoot biomass by weighing the whole plant. Total kernel weight and kernel number per plant were recorded after the ear/s was/were removed and manually threshed.

Distance between consecutive plants was also recorded to evaluate the real plant population on the selected portion of the row and to calculate the mean distance between a plant and its contiguous neighbors in the row.

2.3. Calculations and statistical analysis

Individual kernel weight (KW) was estimated as the ratio between yield per plant (Y_p) and kernel number per plant (KN_p). Likewise, the harvest index (HI) was estimated as the ratio between grain yield per plant and shoot biomass per plant (B_p). To calculate HI, the grain yield per plant was adjusted to 0 g kg⁻¹ moisture.

The mean distance (MD) between a plant and its contiguous neighbors in the row was calculated as:

$$MD_i \text{ (m)} = \frac{D_1 + D_2}{2} \quad (1)$$

where MD_i is the MD of the plant i , D_1 is the distance between the plant i and the plant $i - 1$ and D_2 is the distance between the plant i and the plant $i + 1$.

The yield per unit area was calculated as the sum of grain yield per plant in the area calculated based on the sum of the MD of each plant. The reported grain yield per plant (g plant⁻¹) and grain yield per unit area (g m⁻²) were corrected to 145 g kg⁻¹ moisture.

Additional yield per unit area was also recorded from the whole plot (10 m²) because plots were also used to develop local fertilizer recommendations. There was a strong association ($P < 0.0001$; $r = 0.89$) between yield per unit area recorded both on 15–20 plants and that recorded on the whole plot.

To classify the plants within a hierarchical group, we followed the method proposed by Maddonni and Otegui (2004). Briefly, we ranked the B_p at physiological maturity in each plot, and then classified plants as dominant or dominated when their B_p was in the uppermost or lowermost 33% of the distribution of the data, respectively.

Absolute response to N was estimated as:

$$\text{Absolute response to N} = X_{\text{fertilized}} - X_{\text{control}} \quad (2)$$

where X represents grain yield per plant, grain yield per unit area, B_p , HI, KN_p or KW.

Response to N relative to the controls, i.e. the percentage of increase for the effect of N, was estimated as:

$$\text{Response to N (\%)} = \left(\frac{\text{Absolute response to N}}{X_{\text{control}}} \right) \times 100 \quad (3)$$

where X represents grain yield per plant, grain yield per unit area, B_p , HI, KN_p or KW.

As a measure of plant stand variability, we calculated the coefficient of variation for grain yield per plant.

Analysis of variance was performed for each experiment using PROC MIXED included in the SAS package (SAS Institute, 2003). Least-squares means tests were performed when treatments effects were significant ($P < 0.05$). Regression and correlation analysis were performed to study the relationships between variables, across all experiments, using PROC CORR and PROC REG (SAS Institute, 2003). The slopes of the linear regressions were compared using dummy variables and a t -test. When the intercept of the linear regression was not significant ($P > 0.05$), functions were fitted considering the intercept equal to 0.

3. Results

3.1. Response to N supply at the crop level

Absolute response to N of grain yield per unit area was significant ($P < 0.05$) in most of the experiments (9 out of 11), except in Exps. 7 and 11 (Table 2). The actual increase in yield per unit area in response to N ranged from ca. 270 (Exps. 10 and 6) to 505 g m^{-2} (Exp. 9). No $N \times$ plant population interaction was detected in Exps. 3, 10 and 11 ($P > 0.1$), whereas the effect of plant population was significant ($P < 0.001$) in Exps. 10 and 11.

Although there was no significant $N \times$ plant population interaction for grain yield per unit area in Exps. 3, 10 and 11 (Table 2), absolute response to N was consistently higher in the high plant population as compared with the low density (Exp. 3: 239 vs 326 g m^{-2} ; Exp. 10: 164 vs 385 g m^{-2} ; Exp. 11: 17 vs 112 g m^{-2}).

In general, kernel number mimicked grain yield (Table 2), whereas kernel weight (KW) was increased by N in four out of eleven experiments (Table 2). Shoot biomass was less responsive to N than grain yield (in average 38 vs 58%, respectively) and ranged from 970–2100 g m^{-2} in controls to 1450–2800 g m^{-2} in fertilized treatments (Table 2).

Pooling all the experiments, N addition increased HI by 15%, whereas the response of HI to N was significant ($P < 0.05$) only in Exps. 3, 4, 5, 9 and 10 (Table 2). Kernel number per unit area and KW were associated with grain yield ($P < 0.001$; $r = 0.84$ and $r = 0.62$, respectively). The association of shoot biomass and harvest index with grain yield per unit area was also significant ($r = 0.76$, $P < 0.0001$ and $r = 0.51$, $P < 0.01$, respectively).

3.2. Response to N at the plant level

Both grain yield per plant and grain yield per unit area were similarly affected by N supply (Table 3). Unlike grain yield per unit area, grain yield per plant differed between plant densities in Exp. 3 (Table 3).

The absolute response to N of grain yield per plant ranged from 26 (Exp. 2) to 72 g plant^{-1} (Exp. 1), and was closely associated ($P < 0.0001$) with the absolute response at the crop level.

The coefficient of variation of grain yield per plant was reduced ($P > 0.05$) by the effect of N in Exps. 3, 6, 9 and 10, although it tended to be consistently lower in fertilized treatments, except in Exps. 2 and 5 (Table 3). In Exp. 10, the reduction of coefficient of variation (CV) by the effect of N was higher in the high density treatment, i.e. a significant $N \times$ plant population interaction ($P < 0.05$) was detected.

Grain yield per plant was negatively associated ($P < 0.01$) with CV of yield per plant across all the experiment, i.e. the higher the CV, the lower the Y_p . The coefficient of variation ranged from 18 to 56%, whereas grain yield per plant ranged from 38 to 181 g plant^{-1} , reflecting the wide range of stand variability and growing conditions of the experiments.

The coefficient of variation of the mean distance (MD) ranged from 4 to 41% and did not account for the variation of CV of Y_p . Likewise, there was no association between grain yield per plant and MD.

3.3. Response to N in contrasting hierarchies

Response to N of grain yield per plant was associated with B_p in controls (Fig. 1), tending to be higher with smaller plants. The increase of B_p in controls reduced the response to N, in a curvilinear shape in dominated plants, and in a linear shape in dominant plants.

The response to N of dominated plants was as high as 100–240% for values of average plant biomass in controls lower than 100 g plant^{-1} . In the range of plant size from ca. 150 to 250 g plant^{-1} in controls, the response to N did not differ between plant hierar-

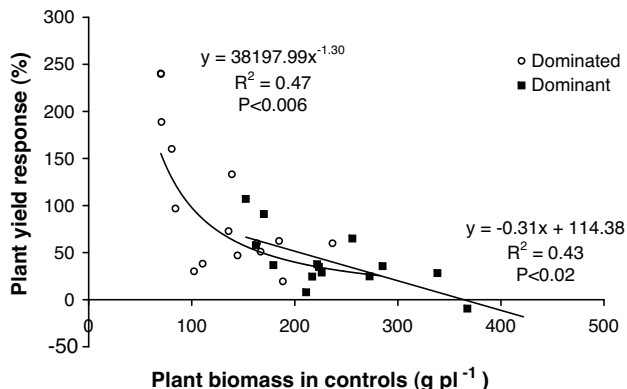


Fig. 1. Plant yield response to N as a function of plant biomass in control plots. Closed symbols: dominant plants. Open symbols: dominated plants.

chies. The response to N in dominant plants tended to be negligible at ca. 350 g plant^{-1} in controls (Fig. 1).

The reduction in CV of grain yield per plant was negatively related ($P < 0.01$) to response to N in dominated plants (Fig. 2), although the relationship was mainly driven for plants with N response $> 150\%$. This result suggests that the increase in grain yield per plant of dominated plants reduces stand variability. The reduction of CV as affected by N was not related to the response to N in dominant plants (Fig. 2).

The coefficient of variation of grain yield per plant was negatively related ($P < 0.0001$) to the ratio between B_p of dominated and dominant plants (Fig. 3), i.e. stands with a smaller difference between sizes of plant types showed a lower CV. The ratio between B_p of dominated and dominant plants, in turn, was positively related to B_p of dominated plants ($P < 0.0001$; $R^2 = 0.58$) and unrelated ($P > 0.05$) to B_p of dominant plants, thus suggesting that differences in biomass between plant types arose from a more than proportional size reduction in dominated plants when N availability and growing conditions were limiting.

3.4. Contribution of dominated and dominant plants to the response to N of the grain yield per unit area

The response to N of the grain yield per unit area was related ($P < 0.0001$) to the response to N of dominant and dominated plants (Fig. 4). However, at high response levels ($> 50\text{--}60\%$) of grain yield per unit area, dominant plants had a considerably lower response than dominated plants, i.e. the slope of the regression differed between dominant and dominated plants.

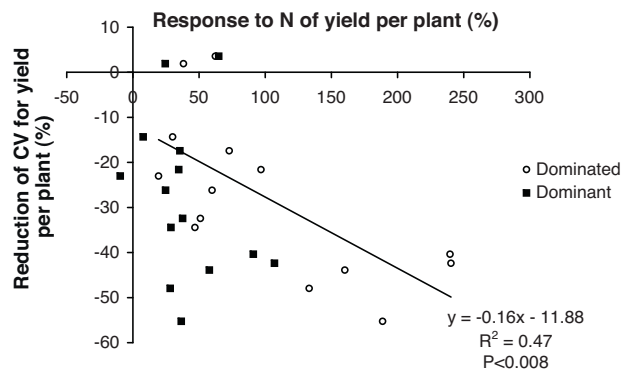


Fig. 2. Relationship between reduction in the coefficient of variation (CV) of yield per plant and the response to N in dominated and dominant plants of 11 experiments. The fitted function represents the linear relationship between variables only for dominated plants.

Table 2

Grain yield, Kernel number per unit area, kernel weight, shoot biomass and harvest index for fertilized and control treatments of maize experiments carried out in Paraná, Argentina from 2002/03 to 2007/08 cropping seasons.

Experiment	Treatment	Grain yield ^a (g m ⁻²)	Kernel number (# m ⁻²)	Kernel weight (mg)	Shoot biomass (g m ⁻²)	Harvest index ^b (g g ⁻¹)
1	0 kg N ha ⁻¹	479b	2312b	0.206b	1046b	0.39a
	140 kg N ha ⁻¹	923a	3738a	0.247a	1736a	0.45a
2	0 kg N ha ⁻¹	703b	3150a	0.223b	1341a	0.45a
	50 kg N ha ⁻¹	693b	2995a	0.232ab	1329a	0.45a
3	200 kg N ha ⁻¹	944a	3868a	0.243a	1677a	0.48a
	0 kg N ha ⁻¹	576b	2918b	0.198b	1259b	0.39b
	140 kg N ha ⁻¹	859a	3843a	0.226a	1679a	0.44a
	4 plants m ⁻²	685A	2953B	0.230B	1388A	0.42A
4	8 plants m ⁻²	750A	3808A	0.195A	1549A	0.41A
	0 kg N ha ⁻¹	468b	2330b	0.203a	971b	0.41b
5	140 kg N ha ⁻¹	944a	4105a	0.230a	1753a	0.46a
	0 kg N ha ⁻¹	744b	3577b	0.207b	2096b	0.30b
6	140 kg N ha ⁻¹	1224a	4794a	0.256a	2840a	0.37a
	0 kg N ha ⁻¹	808b	3293b	0.244a	1616a	0.43a
7	140 kg N ha ⁻¹	1087a	4174a	0.258a	2016a	0.46a
	0 kg N ha ⁻¹	354a	2397b	0.145a	1795b	0.17a
8	140 kg N ha ⁻¹	521a	3886a	0.134a	2036a	0.22a
	0 kg N ha ⁻¹	921b	4053a	0.228a	1840b	0.43a
9	140 kg N ha ⁻¹	1223a	4858a	0.252a	2407a	0.43a
	0 kg N ha ⁻¹	415b	2551b	0.163a	1086b	0.33b
10	140 kg N ha ⁻¹	920a	4720a	0.195a	1883a	0.42a
	0 kg N ha ⁻¹	486b	2565b	0.191a	1112b	0.37b
	140 kg N ha ⁻¹	761a	4186a	0.183a	1458a	0.45a
	4.5 plants m ⁻²	577B	2813B	0.205A	1092B	0.45A
11	10 plants m ⁻²	670A	3938A	0.169B	1478A	0.39B
	0 kg N ha ⁻¹	818a	3371a	0.247a	1639a	0.43a
	140 kg N ha ⁻¹	882a	3523a	0.257a	1713a	0.44a
	4.5 plants m ⁻²	742B	2669B	0.278A	1410B	0.45A
	10 plants m ⁻²	958A	4225A	0.226B	1942A	0.42B

Upper case letters are appropriate for mean comparison between plant populations in Exps. 3, 10 and 11 within experiments. Lower case letters are for N rate levels comparison within experiments.

^a 145 g kg⁻¹ moisture.

^b To calculate harvest index the grain yield was adjusted at 0 g kg⁻¹ moisture.

Table 3

Mean and coefficient of variation (CV) of yield per plant, biomass per plant and, mean distance between a plant and its contiguous neighbors for fertilized and control treatments of maize experiments carried out in Paraná, Argentina from 2002/03 to 2007/08 cropping seasons.

Experiment	Treatment	Yield per plant ^a (g plant ⁻¹)	CV (%)	Biomass per plant (g plant ⁻¹)	CV (%)	Mean distance (m)	CV (%)
1	0 kg N ha ⁻¹	52b	37	115b	32	0.16a	36
	140 kg N ha ⁻¹	125a	21	234a	21	0.19a	41
2	0 kg N ha ⁻¹	86b	35	164b	31	0.18a	23
	50 kg N ha ⁻¹	87b	46	167b	34	0.18a	23
3	200 kg N ha ⁻¹	112a	36	199a	27	0.17a	18
	0 kg N ha ⁻¹	94b	465*	203b	40	0.23a	24
	140 kg N ha ⁻¹	142a	30*	278a	28	0.24a	17
	4 plants m ⁻²	149A	32	302A	30	0.31A	18
4	8 plants m ⁻²	86B	43	179B	38	0.17B	22
	0 kg N ha ⁻¹	58b	42	120b	33	0.18a	20
5	140 kg N ha ⁻¹	112a	24	208a	22	0.17a	17
	0 kg N ha ⁻¹	78b	28	221b	17	0.15a	18
6	140 kg N ha ⁻¹	132a	29	306a	20	0.15a	22
	0 kg N ha ⁻¹	94b	27*	188b	24	0.17a	24
7	140 kg N ha ⁻¹	125a	18*	231a	17	0.16a	28
	0 kg N ha ⁻¹	39a	39	195b	14	0.21a	4
8	140 kg N ha ⁻¹	57a	26	222a	14	0.21a	5
	0 kg N ha ⁻¹	110b	29	220b	24	0.23a	34
9	140 kg N ha ⁻¹	147a	21	291a	18	0.23a	28
	0 kg N ha ⁻¹	46b	55*	119b	40	0.21a	25
10	140 kg N ha ⁻¹	101a	33*	207a	27	0.21a	28
	0 kg N ha ⁻¹	77b	49*	168b	38	0.31a	23
	140 kg N ha ⁻¹	118a	30*	222a	26	0.31a	25
	4.5 plants m ⁻²	129A	38	245A	31	0.43A	22
11	10 plants m ⁻²	66B	41	146B	32	0.19B	25
	0 kg N ha ⁻¹	114a	43	222a	32	0.28a	16
	140 kg N ha ⁻¹	118a	35	228a	30	0.27a	18
	4.5 plants m ⁻²	151A	34	287A	28	0.39A	14
	10 plants m ⁻²	81B	44	164B	35	0.16B	21

Upper case letters are appropriate for mean comparison between plant populations in Exps. 3, 10 and 11 within experiments. Lower case letters are for N levels comparison within experiments.

* CV differs significantly ($P < 0.05$) between N rates within each experiment.

^a 145 g kg⁻¹ moisture.

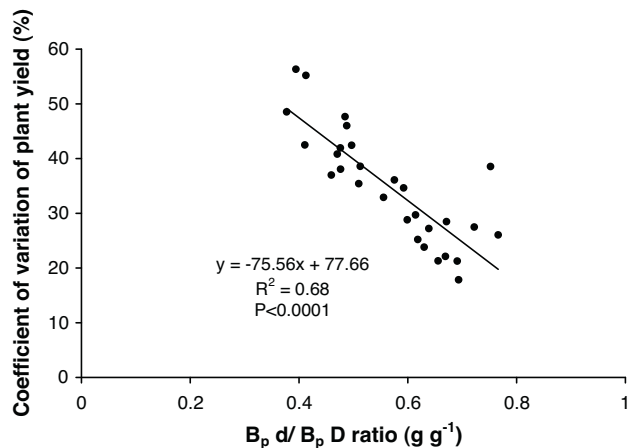


Fig. 3. Relationship between the coefficient of variation of yield per plant and the ratio between biomass per plant (B_p) of dominated and dominant plants ($B_p d/B_p D$ ratio).

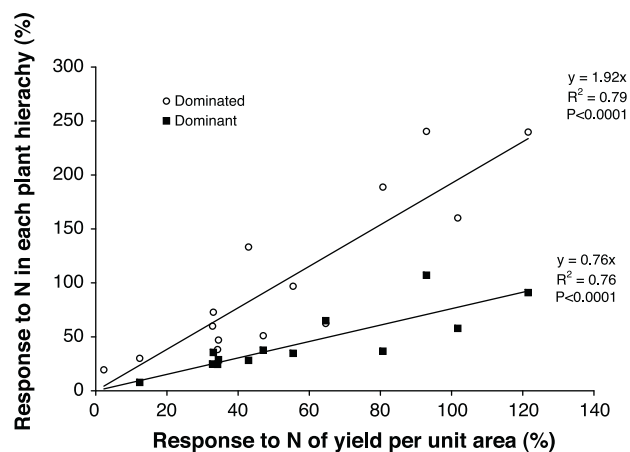


Fig. 4. Response to N of grain yield per unit area (Y_a) as a function of response to N of each plant hierarchy, i.e. dominated and dominant plants. Closed symbols: dominant plants. Open symbols: dominated plants.

At low response levels of grain yield per unit area (<30%), however, plant hierarchies tended to have a similar response to N, because the intercept of linear relationships did not differ from 0 ($P > 0.1$) (Fig. 4). Differences between plant types in the response to N tended to be negligible in more equilibrated stands (Fig. 5), i.e. in those in which the ratio between B_p of dominated and dominant plants in controls was closer to 1.

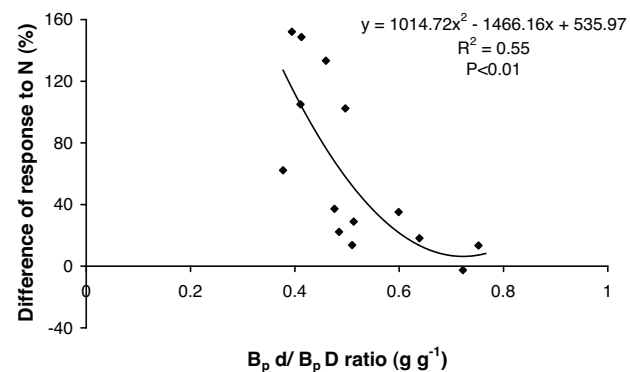


Fig. 5. Absolute difference between response to N of dominant and dominated plants as a function of the ratio between biomass per plant (B_p) of dominated and dominant plants ($B_p d/B_p D$ ratio) in controls.

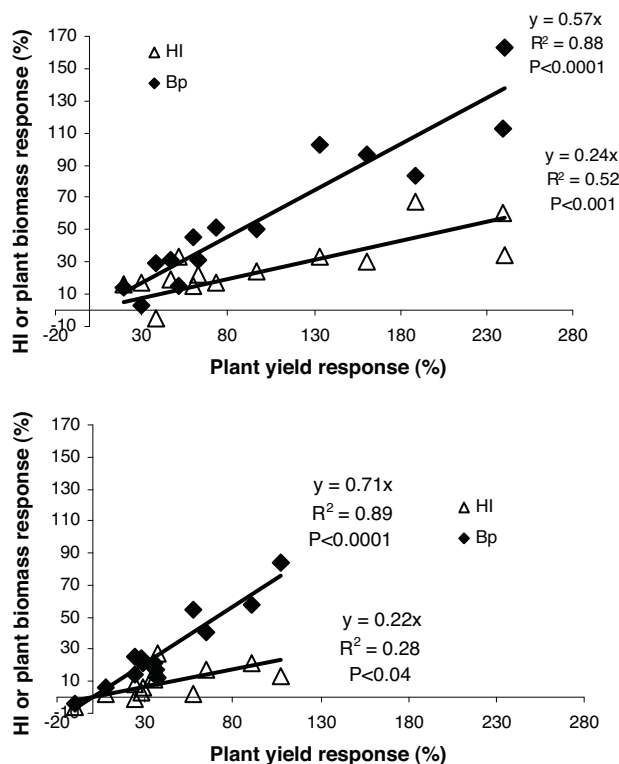


Fig. 6. Response to N of harvest index (HI) and biomass (B_p) as a function of response to N of yield per plant in (A) dominated and (B) dominant plants.

3.5. Response to N of yield components in contrasting hierarchies

The grain yield response to N in both plant hierarchies was related to the response to N in shoot biomass and HI (Fig. 6), although in dominated plants (Fig. 6a) the response in HI accounted for a greater portion of the response to N than in dominant plants (59 vs 32%; $P < 0.0001$; $P < 0.05$, respectively) (Fig. 6b). Also, the slope of the relationship between the response to N and the response in B_p was higher ($P < 0.05$) in dominant plants, i.e. a similar response to N level led to a higher response in B_p in dominant than in dominated plants.

Likewise, the response to N in each plant hierarchy was differentially associated with numerical components (Fig. 7). Dominated plants had a higher response in KN_p at similar levels of response of grain yield per plant than dominant plants, i.e. plant hierarchies differed in the slope of the relationship between the response of grain yield per plant and KN_p . The response to N of KW was associated with the response of grain yield per plant in dominant plants (Fig. 7b), without an evident ($P > 0.1$) response in dominated plants (Fig. 7a).

4. Discussion

4.1. Response to N at the crop and at the plant levels

Our experimental conditions included a wide range of maize yields and responses to N (Tables 2 and 3), indicative of the extent of variation in intra-specific competition among plants within the stand, as a result of different N availability and environmental conditions, since the plant population was not modified between fertilization treatments within experiments, with the exception of Exps. 3, 10 and 11 which had intentional plant population differences (Table 1).

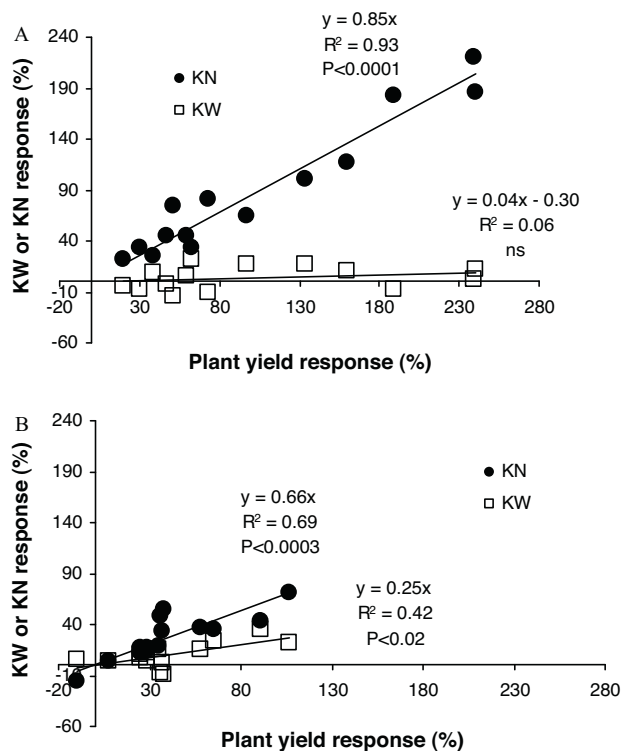


Fig. 7. Response to N of kernel number per plant (KN_p) and kernel weight (KW) as a function of response to N of yield per plant (Y_p) in (A) dominated and (B) dominant plants.

At the crop level, our results were consistent with previous findings (e.g. Lemcoff and Loomis, 1986; Uhart and Andrade, 1995; Boomsma et al., 2009). In general, N supply increased either one or a combination of the following variables: biomass, harvest index, yield and yield components (Table 2). The magnitude of the response of yield to N was probably associated with the initial N availability in the soil (data not shown) and the growing conditions during the cycle. The response to N was not associated with the yield of the controls; for instance, yield of non-fertilized controls ranged from ca. 350 in Exp. 7 to 920 $g\ m^{-2}$ in Exp. 8, but the response was significant only for the latter.

At the plant level, the response to N was dependent on B_p in controls, i.e. a measure of environmental conditions during the cropping season, including availability of resources for crop growth such as water, solar radiation and soil N. The response to N in dominated plants was higher with values of B_p lower than ca. 100 $g\ plant^{-1}$.

Plant growth rate (PGR) in maize has been reported as linearly related to B_p at the onset of the critical period (± 15 d around silking) using a data set with a narrow, low range of PGR in crowded plants (Vega and Sadras, 2003), typical of smaller, dominated plants (Maddonni and Otegui, 2004). Therefore, the greater responsiveness of dominated plants at low B_p levels (Fig. 2), close to the minimum threshold to kernel set, may be related to an increase in their PGR conducive to a considerable impact on KN_p (Fig. 7a).

The moderate and lower response to N at intermediate and higher B_p values, respectively, recorded in both plant types (Fig. 1), would in turn be related to a lower or negligible slope of the relationship between PGR and KN_p expectable at those B_p values.

Growing conditions conducive to a higher intra-specific competition, i.e. low PGR around silking, lead to remarkable differences among individuals within the stand (Glenn and Daynard, 1974; Edmeades and Daynard, 1979; Maddonni and Otegui, 2004). The impact of intra-specific competition on the alteration of size struc-

ture of the population can be quantified by the ratio between B_p of dominated (d) and dominant (D) plants ($B_p\ d/B_p\ D$ ratio). Our results showed that the $B_p\ d/B_p\ D$ ratio exhibited a negative relationship with the CV of grain yield per plant (Fig. 3).

Although the increase in stand variability as interplant competition increases has been early and profusely documented (Glenn and Daynard, 1974; Maddonni and Otegui, 2004; Andrade and Abbate, 2005), improvement of the stand equality in maize by effect of an abiotic factor as N has been only recently reported (Boomsma et al., 2009).

Contribution of each plant type to the overall stand response to N (Fig. 4) and to the reduction of the CV (Fig. 2) was different and associated with the $B_p\ d/B_p\ D$ ratio in the controls (Fig. 5), i.e. a measure of the intra-specific-driven size structuring process.

The differential response of dominated and dominant plants to N is related to the $B_p\ d/B_p\ D$ ratio and there was either no response or a small differential response when the two groups were similar (Fig. 5). Hence, we inferred that the response of each plant hierarchy depended on the extent of the size structuring process in the population, i.e. the $B_p\ d/B_p\ D$ ratio, which would in turn be related to the resource availability per plant during the cropping season. Accordingly, the calculations obtained from the results of Maddonni and Otegui (2004) demonstrated that the high competition levels obtained by manipulating the plant population lead to a high size structuring progress, i.e. the $B_p\ d/B_p\ D$ ratio increased from 0.54–0.56 to 0.69–0.75 as plant density was reduced from 12 to 6 $plant\ m^{-2}$.

Attenuations in plant interference through reductions in plant population or spatio-temporal variability have been observed to result in lower plant-to-plant variability in a way similar to that shown by our results (Glenn and Daynard, 1974; Maddonni and Otegui, 2004; Liu et al., 2004a).

Competition for light has been commonly considered asymmetric, i.e. larger individuals have a disproportionately greater advantage to use the available resource than smaller ones (Weiner, 1990), but Vega and Sadras (2003) have suggested a more symmetric competition in maize than in sunflower and soybean, based on plant population experiments. However, our results are indicative of a strong asymmetric competition, revealing a disproportionate advantage of dominant plants, as evidenced by the reduced $B_p\ d/B_p\ D$ ratio in controls in the highly responsive experiments.

Stand variability in maize has been attributed to several reasons, including uneven emergence, uneven plant spacing in the row, seed and seedling size, and micro-environment variation (e.g. Nafziger et al., 1991; Andrade and Abbate, 2005). However, Maddonni and Otegui (2004) have reported a CV of B_p as high as 20–50%, even in stands homogeneous in time to emergence, plant spacing and seed size.

The effect of stand variability on yield per unit area was early reported by Glenn and Daynard (1974). Also, there is a considerable amount of research on causes of variability such as plant distance and uneven emergence (Nafziger et al., 1991; Liu et al., 2004a,b). Likewise, a negative relationship between grain yield per plant and stand variability (CV of vegetative biomass per plant) has been documented (Andrade and Abbate, 2005). Our results support those findings in a broader range of grain yield per plant (two fold, 39–180 $g\ plant^{-1}$).

4.2. Response to N of yield per plant components

Tollenaar et al. (2006) associated the reduction of yield of crowded plants of evenly emerged stands with an inferior ability to capture resources (B_p). They also found that non-crowded plants can offset that reduction by increasing B_p , proportionally resulting in no differences in yield at the crop level. However, in crowded plants with emergence delay, Tollenaar et al. (2006) attributed the

reduction in grain yield per plant to a lower resource capture (B_p) and resource utilization (HI) not compensated by non-crowded plants, reducing yield at the crop level.

In our study, response to N of grain yield per plant in dominated plants was associated with the response in B_p and HI (Fig. 6a), whereas in dominant plants the response to N of grain yield per plant was associated mainly with the response in B_p (Fig. 6b).

Two possible causes could account for the strong response to N of B_p and HI in dominated plants under responsive conditions: (i) delayed emergence (Tollenaar et al., 2006) or (ii) high levels of plant interaction. Although the crops were not manually sown, all the stands were evenly emerged (<4 d between the emergence of the first and the last coleoptile). Therefore, the response of B_p and HI to N in dominated plants should be related both to their small size resulting from the intense structuring process in the population under our experimental conditions and to the particular shape of the relationship between the B_p and HI reported for maize (Vega et al., 2000; Echarte and Andrade, 2003; Vega and Sadras, 2003).

In fact, the thresholds of B_p to reach the maximum HI (Vega et al., 2000; Echarte and Andrade, 2003) and PGR (Tollenaar et al., 1992; Andrade et al., 1999) to reach the maximum KN_p lead to the magnification of differences between extreme plant hierarchies under high plant-interference conditions, i.e. poor growing conditions during the critical period. Therefore, the higher response to N in plants with low B_p plants may indicate that they were under thresholds of B_p and PGR to reach maximum HI and KN_p .

Accordingly, a high response to N of B_p in dominant plants, coupled to a positive response in vegetative B_p (not shown), suggests that this plant type had a B_p up to the threshold to reach the maximum and a more stable HI for the evaluated genotypes.

The response to N of KN_p , without response of KW, in dominated plants (Fig. 7a) would indicate growth under the minimum PGR threshold to reach the maximum KN_p .

4.3. Agronomic implications

Due to its economic and environmental implications, nitrogen use efficiency (NUE) is becoming a critical issue to reach system sustainability. Our results reveal that agronomic strategies of plant density reduction as a way to decrease the competition level led to a lower NUE, as evidenced by the lower response to N in low plant density (Exps. 3, 10 and 11). A lower stand response to N at a given N rate is indicative of a lower NUE, since NUE is estimated as the ratio between absolute response (Eq. (2)) and N rate. Similar results have been previously found by Lemcoff and Loomis (1986) and Boomsma et al. (2009), who reported an increased response to N or NUE associated with an increase in plant density. In contrast, Shapiro and Wortmann (2006) did not find a better response to N across plant densities, but used a narrower range of plant density (ca. 6.2–8.7 plants m^{-2}) than in the works carried out by Lemcoff and Loomis (1986), Boomsma et al. (2009) and ourselves.

The lower response to N in low plant density could be related to: (i) an equilibrated response of extreme plant hierarchies, as a result of a lower $B_p d/B_p D$ ratio, (ii) the morphogenetic limitation of maize to linearly increase its grain yield per plant as growing conditions are improved, (iii) a lower N absorption efficiency, as compared with high plant density, associated with higher root exploration. In relation with this, Barbieri et al. (2008) have suggested that the improved NUE in narrow rows is related to a better N capture through an increased root exploration.

In the light of the novel development of precision agriculture, it has been demonstrated that a finer resolution scale of N management may increase NUE (Tubaña et al., 2008). Even more, in-season-by-plant N fertilization in maize has also been suggested (Martin et al., 2005). Here we demonstrated that, under responsive conditions, all plants of the stand contribute to the overall response,

in a variable extent depending on the level of interplant competition, suggesting that the N rate should be increased in dominated plants within the stand, in which we observed the highest response to N.

However, a recent study in which individual plants were fertilized with labeled N reported that N uptake of neighboring plants (adjacent at ca. 0.18 m to the N source) can be as high as 32–40% of the N added to a single plant (Hodgen et al., 2009). Therefore, technologies based on plant-to-plant N fertilization applied on the soil should not be encouraged as a way to increase NUE.

5. Conclusions

Response to N of grain yield per plant differed between dominated and dominant plants, depending on the biomass at maturity in non-fertilized controls. The increase in the biomass at maturity in non-fertilized controls reduced the response to N in a curvilinear shape in dominated plants, and in a linear shape in dominant plants. The more proportional response in dominated plants than in dominant ones led to a reduction in the stand variability across experiments.

The plant types differed in their contribution to the response to N of grain yield per unit area, mainly at higher level of response (>50–60%). At lower level of response (<30%), the contribution of contrasting plant hierarchies was similar.

When the differences in biomass at maturity between dominated and dominant plants were ample, the responses to N at the stand level were highest, as a result of the increase in grain yield per plant mediated through higher B_p and HI, although these increases differed between dominated and dominant plants.

Acknowledgments

We thank Victor Sadras and Fernando Andrade for their valuable comments and suggestions on an early version of the manuscript. Technical assistance of the staff of the Natural Resources Group of EEA Paraná is gratefully acknowledged. This work was funded by INTA (Projects E.RIOS02/61:630021 and AEAI273221) and PICT2007-00483. O. Caviglia is a member of CONICET, the Research Council of Argentina.

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