Response of Maize and Soybean to Variability in Stand Uniformity

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ABSTRACT

The literature indicates variable results in response to uneven stands. We tested the hypothesis that the effect of uneven stands on grain yield varies depending on the vegetative and reproductive plasticity of the species and cultivars. Treatments consisted of a uniform control, nonuniform plant spacing between plants, and uneven seedling emergence. For maize (*Zea mays* L.), average yield per plant (Yp) decreased 0.68 g for every unit increase in percentage coefficient of variation (CV) for vegetative biomass per plant (Vp). Contrarily, soybean [*Glycine max* (L.) Merr.] Yp was not affected by increments in plant size variation. A model based on the relationship between Yp and Vp and on mean and CV for Vp was used to estimate the effect of nonuniformity on grain yield in maize and soybean cultivars. Based on these models and assuming constant average Vp with a normal frequency distribution throughout different stand uniformity treatments, increases in CV for Vp resulted in less grain yield in maize but not in soybean. Reductions in vegetative biomass produced further yield drops according to the specific relationship between Yp and Vp. The effect of unevenness in plant sizes on maize grain yield would depend on the characteristics of the hybrid. A stable hybrid is characterized by low decreases in Vp in response to heterogeneity, low threshold Vp for prolificacy and for grain yield, and a low curvature in the Yp/Vp relationship.

Nonuniform stands at constant plant density could result from variation in time of plant emergence and in plant spacing. Variation in planting depth, nonuniform surface crop residue distribution in no-tillage systems, microsite variation in the seed bed condition, and seed vigor are major factors responsible for uneven time of seedling emergence in the field. On the other hand, planters with low precision in seed placement and careless planting operation are the main causes of variable gap size between plants within the row in stands of equivalent mean plant density. Early signals allow plants to detect the presence of neighbors and respond to them by, for instance, increasing the rate of internode elongation and changing the pattern of dry matter allocation (Aphalo and Ballaré, 1995; Ballaré et al., 1994). Small differences in plant size during early plant development are usually amplified as the season progresses and competition for resources intensifies (Maddonni and Otegui, 2004).

The literature indicates variable results in response to uneven stands. Negative effects of uneven emergence on grain yield were found in maize (Nafziger et al., 1991; Tollenaar and Wu, 1999; Liu et al., 2004a) but not in soybean (Egli, 1993a). Moreover, nonuniform within-row plant spacing resulted in lower maize yield in some cases (Krall et al., 1977; Vanderlip et al., 1988) but not in others (Erbach et al., 1972; Muldoon and Daynard, 1981; Liu et al., 2004b). The effects of uneven stands likely vary depending on the species and the genotypes and according to the environmental conditions. An analysis of morphophysiological traits at the individual plant level may be necessary to improve the understanding of the effect of nonuniform stands on crop yield. Soybean plants have higher vegetative plasticity in response to increments in space or resources per plant than maize plants (Carpenter and Board, 1997; Valentinuz, 1996). Moreover, soybean showed greater reproductive plasticity and harvest index stability than maize in response to variation in shoot biomass (Vega et al., 2000). The vegetative plasticity and the relationship between Yp and shoot biomass also differ among cultivars within a species. For instance, Echarte and Andrade (2003) concluded that modern maize hybrids showed higher harvest index stability than older hybrids mainly because of lower biomass threshold for grain yield and higher reproductive plasticity in response to increases in resources per plant.

We tested the hypothesis that the effect of uneven stands on grain yield varies depending on morphophysiological traits of the species and cultivars. The effect of stand variability on grain yield would be largest for maize and smallest for soybean because of the lower reproductive and vegetative plasticity of the former species. Within maize cultivars, the effect of uneven stands would be larger for cultivars with high biomass threshold for grain set and low reproductive plasticity in response to increases in resources per plant.

MATERIALS AND METHODS

Experiments and Measurements

The data were obtained from four experiments conducted at the Instituto Nacional de Tecnología Agropecuaria Balcarce Experimental Station (37°45′ S, 58°18′ W; 130 m altitude), during the 2001–2002 and 2002–2003 growing seasons. The soil was a fine-loamy, mixed, thermic Typic Argiudoll with a minimum effective depth of 1.5 m and with an organic matter content of approximately 5.6% in the top 25 cm of depth. The area is characterized by low average temperatures during the growing season (17.8°C) and a frost-free period of about 150 d. More details about the climatic regime of the Balcarce region

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Abbreviations: Bp, total aboveground biomass per plant; CV, percentage coefficient of variation; SD, standard deviation; Vp, vegetative biomass per plant; $\overline{X}$, mean; Yp, yield per plant.

were presented in Andrade (1995). Maize hybrid DK752 in Exp. 1 and 2 was planted at the optimal date (mid-October) and in Exp. 3 in early November. In all cases, final density was around 8 plants m^{-2}. Soybean cultivar A3901 was planted in early November (Exp. 4) with a final plant density of 40 plants m^{-2}. Soybean seeds were inoculated with *Bradyrhizobium japonicum*. The experiments were conducted with three replications. The size of the plots was three rows 0.70 m apart and 12 m long. Plots were fertilized with 30 kg P ha^{-1} to provide adequate P nutrition. Maize crops were fertilized with 140 kg N ha^{-1} at V6 stage. In all experiments, irrigation was applied to keep soil water over 50% of maximum soil available water in the first meter of depth during the entire growing season. Weeds and insects were adequately controlled.

In Exp. 1 and 4, treatments consisted of a uniform control, nonuniform plant spacing between plants, and uneven seedling emergence. In Exp. 2, treatments were a uniform control, nonuniform plant spacing between plants, and a combination of nonuniform plant spacing and uneven seedling emergence. Finally, Exp. 3 consisted of a uniform control and two levels of uneven seedling emergence. In maize and soybean, plant-spacing treatments were achieved by thinning within a week after emergence to the target density and distribution. In maize, variability in seedling emergence was achieved by sequential plantings and thinning after emergence. In soybean, variability in seedling emergence was achieved by thinning for either uniform and nonuniform seedling sizes within a single planting date. Distances between plants were recorded. Plant spacing standard deviation (SD) was around 2 cm for the maize control, 2.8 cm for the soybean control, 5.4 cm for the nonuniform soybean treatment, and 7 to 12 cm for the nonuniform maize treatment. The range in seedling emergence was less than 3 d for the control treatments and 7 to 8 d for the uneven emergence treatments.

In each plot, approximately 20 consecutive plants of the central row were tagged and harvested at maturity. Samples were oven-dried at 60°C to constant weight, and Yp and total aboveground biomass per plant (Bp) were determined. In soybean, aboveground vegetative biomass did not include fallen leaves. Number of grains per plant and individual grain weight were also recorded. The weight of nongrain plant parts was calculated as the difference between Bp and Yp. This was taken as an estimation of Vp. Mean ($\bar{X}$), SD, and CV were calculated for these variables.

Data Analysis

Data were analyzed by ANOVA procedures, standard errors of the means were calculated, and linear regressions between plant yield and CV for Vp were calculated for maize and soybean with data from all experiments and treatments (Steel and Torrie, 1980). Vegetative biomass data were checked for normality after pooling replications using the Chi-squared test (Steel and Torrie, 1980) for accumulated frequency, and skewness and kurtosis were calculated.

Relationships between Yp and Vp for maize hybrid DK752 and soybean cultivar A3901 were obtained from plots independent of Exp. 1 to 4, which were planted at different densities and with nonuniform distribution to obtain a wide range in plant sizes. From these plots, Bp, Yp, and Vp were recorded. Relationships between Yp and Vp for other maize (hybrid M400) and soybean (A3205) cultivars were derived from data presented in the literature (Echarte and Andrade, 2003; Vega et al., 2000). The above relationships were adjusted by Table Curve Software (Jandel Scientific, 1991).

In maize, a curvilinear with plateau equation was fitted to the Yp vs. Vp data,

$$\begin{cases} \text{if Vp} < d \text{ then Yp} = a(\text{Vp} - b)/[1 + c(\text{Vp} - b)] \\ \text{else if Vp} \geq d \text{ then Yp} = a(d - b)/[1 + c(d - b)] \\ \text{else if Vp} < b \text{ then Yp} = 0 \end{cases} \quad [1]$$

where *a* represents the initial slope of the relationship, *b* the Vp threshold for yield (minimum Vp that produces yield), *c* the degree of curvilinearity of the relationship, and *d* the Vp value at which Yp reaches a plateau. When prolificacy was considered, a second curvilinear function was added to Eq. [1] beyond a threshold Vp for prolificacy (b_2). This function includes yield of secondary ears (Yp_2), considering grain yield of these ears and the proportion of prolific plants,

$$\begin{cases} \text{if Vp} > b_2 \text{ then Yp}_2 = a_2(\text{Vp} - b_2)/[1 + c_2(\text{Vp} - b_2)] \\ \text{else Yp}_2 = 0 \end{cases} \quad [2]$$

In soybean, the relationship between Yp and Vp was described by a linear model,

$$\text{Yp} = a + b\text{Vp} \quad [3]$$

where *a* is the ordinate and *b* the slope of the relationship. Examples of Eq. [1] and [3] are presented in Fig. 1.

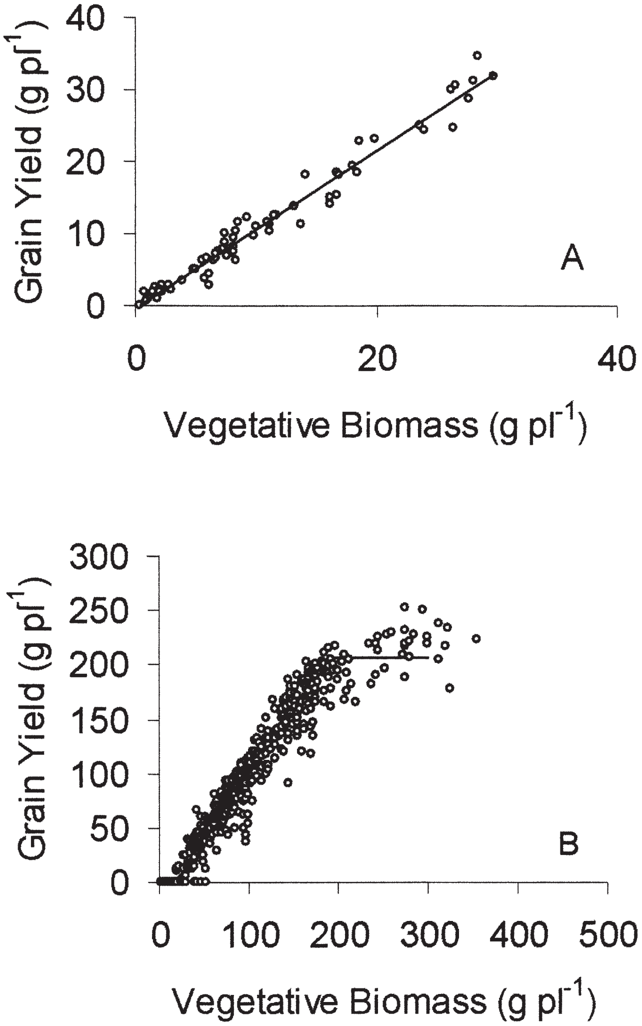

Fig. 1. Relationship between yield per plant and vegetative biomass per plant for (A) soybean cultivar A3901 and (B) maize hybrid DK752. Parameters of Eq. [3] fitted to soybean data were $a = -0.47$ and $b = 1.09$ ($R^2 = 0.970$). Parameters of Eq. [1] fitted to maize data were $a = 1.42$, $b = 18.57$, $c = 0.0012$, and $d = 196.0$ ($R^2 = 0.965$). Each point represents one plant.

Mean plant yield ($\hat{Y}$) was estimated as the sum of Yp resulting from Eq. [1] and [3], weighed by the Vp frequency according to the normal distribution function,

$$\hat{Y} = \sum_{\mathrm{Vp}=\mathrm{Vp}_{\min}}^{\mathrm{Vp}=\mathrm{Vp}_{\max}} [\mathrm{Yp}(\mathrm{Vp}) \times f(\mathrm{Vp}, \overline{X}, \mathrm{SD})] \qquad [4]$$

where $\mathrm{Vp}_{\min}$ and $\mathrm{Vp}_{\max}$ were 0 and $2\overline{X}$, the Yp(Vp) term corresponds to Eq. [1] or [2] for maize and Eq. [3] for soybean, and the second term is the Vp frequency, which is assumed normally distributed,

$$f(\mathrm{Vp}, \overline{X}, \mathrm{SD}) = \left(\frac{1}{\sqrt{2\pi \mathrm{SD}^2}}\right) e^{-(\mathrm{Vp}-\overline{X})^2/2\mathrm{SD}^2} \qquad [5]$$

where $\overline{X}$ and SD are the Vp average and the SD and e is the natural logarithm base.

Yield per plant of each plot in Exp. 1, 2 (maize), and 4 (soybean) were estimated according to Eq. [4], based on mean Vp and its SD, assuming a normal distribution of Vp within each plot. Experiment 3 was not included because late plantings resulted in a different Yp vs. Vp relationship (Cirilo and Andrade, 1994).

The mean root squared error (MRSE) of Y was calculated as

$$\mathrm{SE} = \left[\left(\sum_{i=1}^{i=n} (\hat{Y}_i - Y_i)^2\right) \Big/ n\right]^{1/2} \qquad [6]$$

where $\hat{Y}_i$ and Y_i are the estimated and measured Yp and n is the number of observations. The MRSE and the relationship between the estimated and observed Yp values were used to evaluate the adequacy of the model to predict the effect of uneven stands on crop performance.

RESULTS

Response to Nonuniform Stands

For the control maize treatments, Vp accumulated frequencies were normally distributed ($p > 0.98$) with skewness between 0 and 0.4 and kurtosis between −0.1 and −0.5. In agreement with these results, Edmeades and Daynard (1979) found that shoot weight and leaf area per plant were normally distributed throughout the growing season. Nonuniform treatments resulted in large increases in CV for Vp (Table 1) and in nonconsistent variation in skewness and kurtosis of the Vp frequency distribution, which remained normal ($p > 0.95$). Soybean showed larger CV (Table 1) and kurtosis (−0.9) for Vp in the control treatment than maize, as in Vega and Sadras (2003). However, the Vp accumulated frequencies were also normally distributed ($p > 0.95$). Again, nonuniform treatments increased vegetative weight variation, but the Vp frequency distribution remained normal.

Table 1. Vegetative (Vp) and total aboveground (Bp) biomass per plant and yield per plant (Yp) for control and nonuniform treatments in maize (Exp. 1, 2, and 3) and soybean (Exp. 4). Percentage coefficients of variation are indicated between brackets.

Exp.	Treatment†	Vp	Yp	Bp
			g	
1	Control	161 (15.2)	165 (11.2)	327 (12.1)
	Sp	150 (21.0)	156 (21.1)	303 (20.0)
	Tp	142 (25.4)	146 (24.4)	288 (24.4)
msd‡		14	12	24
2	Control	161 (13.5)	164 (11.6)	325 (12.4)
	Sp	154 (23.4)	152 (22.3)	306 (22.2)
	SpTp	150 (36.0)	148 (34.0)	298 (34.8)
msd		17	27	44
3	Control	161 (12.0)	150 (14.1)	311 (12.4)
	Tp	158 (29.7)	141 (31.1)	299 (29.3)
	Tp	148 (28.6)	132 (31.5)	280 (29.2)
msd		25	10	30
4	Control	10.4 (36.7)	10.4 (39.9)	20.8 (38.1)
	Sp	10.5 (42.7)	10.6 (42.8)	21.1 (42.2)
	Tp	9.8 (48.2)	10.3 (50.8)	20.1 (48.9)
msd		1.7	1.5	3.1

† Sp, spatial nonuniform treatment; Tp, temporal nonuniform treatment.
‡ msd, minimum significant difference.

Increasing variation in plant spacing increased variation in plant biomass and Yp, but it did not affect Yp in both crops (Table 1). When data from the control and the nonuniform spacing treatments were combined, increases in CV for plant spacing resulted in Vp and Yp reduction in maize ($\mathrm{Yp} = -0.219\mathrm{CVs} + 166$; $p < 0.05$) but not in soybean. Nonuniform plant emergence also resulted in larger variation in Bp and Yp in both crops. However, this treatment reduced Yp in maize but not in soybean (Table 1). Significant negative linear relationships between Yp and CV for date of emergence (CVd) were found for maize when data from the control and the nonuniform emergence treatments from Exp. 3 (the only experiment in which emergence was recorded plant per plant) were combined ($\mathrm{Yp} = -0.806\mathrm{CVd} + 156$; $p < 0.05$).

Combining the data from experiments with spatial and temporal variation, average maize Yp decreased 0.68 g for every unit increase in CV for Vp ($r = 0.53$, $p < 0.01$; Fig. 2B). Contrarily, soybean grain yield was not affected by increments in plant size variation (Fig. 2A). However, the range in CV for Vp was larger in maize than in soybean. For these cultivars and growing conditions, heterogeneity in Vp was negatively related to yield in maize but not in soybean.

Relationship between Plant Yield and Vegetative Biomass

In soybean cultivar A3901, the linear relationship between Yp and Vp had a nonsignificant ordinate and a slope of 1.09 (Fig. 1A). In maize hybrid DK752, the plateau of the curvilinear relationship between Yp and Vp began at a Vp value of 196 g, and the threshold Vp value for grain yield was 19 g (Fig. 1B). Only the uppermost ear was considered since no prolific plants were observed for the conditions of Exp. 1, 2, and 3.

Predicting Effects of Nonuniform Stands

The estimated soybean mean plot Yp values calculated with Eq. [4] were not different from the observed values (Fig. 3A). The RMSE was 0.47 g plant^{-1}, and the ordinate and the slope of the linear equation between observed and predicted values did not differ from 0 and 1, respectively. In maize, as it was observed for soybean, the estimated mean plot Yp values calculated with Eq. [4] were not different from the observed values (Fig. 3B). The RMSE was 7.6 g plant^{-1}. This value increased 40% when the estimation was based only on average Vp, disregarding SD. The ordinate and the slope of the linear equation fitted to the data did not differ from 0 and 1, respectively. These results indicate that the model based on the relationship between Yp and Vp and on a normal distribution of Vp was adequate to predict the effects of uneven stands on grain yield. Based on these models and assuming constant average Vp in both crops and no prolificacy in maize, increases in CV for Vp resulted in less grain yield in maize but not in soybean (Fig. 4). In maize, important mean Yp reductions were observed at CV for Vp greater than 30%. Possible reductions in mean Vp could produce further yield drops according to the specific relationship of Yp vs. Vp.

Cultivar Effects

The relationship between Yp and Vp was linear with nonsignificant ordinate intercept for two different soybean cultivars (A3205 and A3901, Fig. 5A). In both cultivars, $\hat{Y}$ (estimated with Eq. [4]) was not affected by increases in CV for Vp. In contrast to soybean, the effect of plant unevenness on maize yield depended on the hybrid. Quite different relationships between Yp and Vp were observed for two maize cultivars (Fig. 5B). Hybrid DK752 presented a lower threshold Vp value for zero Yp and a higher upper-ear reproductive plasticity (flex ear characteristic) than the older hybrid M400 (Echarte and Andrade, 2003). Because of these differences in the Yp vs. Vp relationship, the increase in CV for Vp from 0 to 35% resulted in $\hat{Y}$ decreases (estimated with Eq. [4]) of 4.9% in DK752 (Table 2, Case 2) and 8.4% in M400 (Table 2, Case 3), assuming constant mean Vp and nonprolificacy.

Maize hybrids can differ in prolificacy. The Vp thresholds for prolificacy are much lower in prolific hybrids (for example DK664; Echarte and Andrade, 2003) than in nonprolific ones (for example DK636; Vega et al., 2000). A second curvilinear function $\{Yp_2 = 3.01\ (Vp - 193.84)/[1 + 0.023\ (Vp - 193.84)]\}$, typical of prolific hybrids, was included to account for yield of a secondary ear. An hybrid with a Yp vs. Vp relationship similar to that of DK752 but with a high prolificacy would not be negatively affected by unevenness if Vp is not reduced (Table 2, Case 1).

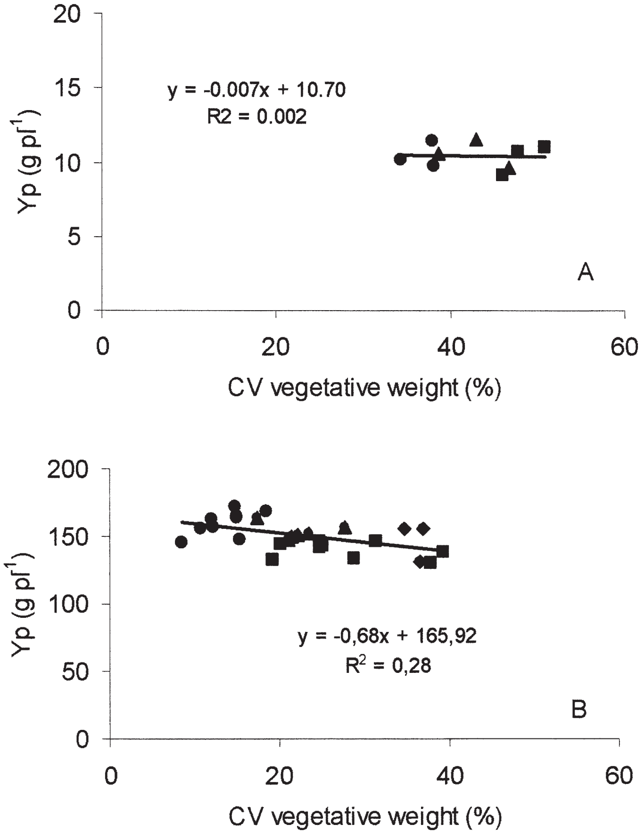

Fig. 2. Relationship between grain yield per plant (Yp) and percentage coefficient of variation (CV) for vegetative biomass per plant (Vp) in (A) soybean and (B) maize. Control (circles), temporal nonuniformity (squares), spatial nonuniformity (triangles), and temporal and spatial nonuniformity (diamonds) treatments are indicated. Data are from Exp. 1, 2, and 3 for maize and Exp. 4 for soybean. Each point represents one experimental unit. For soybean: $y = -0.007x + 10.7$ ($r = 0.045$; ns); for maize, $y = -0.68x + 165.9$ ($r = 0.53$ $p < 0.01$). Plant densities were 40 and 8 plants m^{-2} for soybean and maize, respectively.

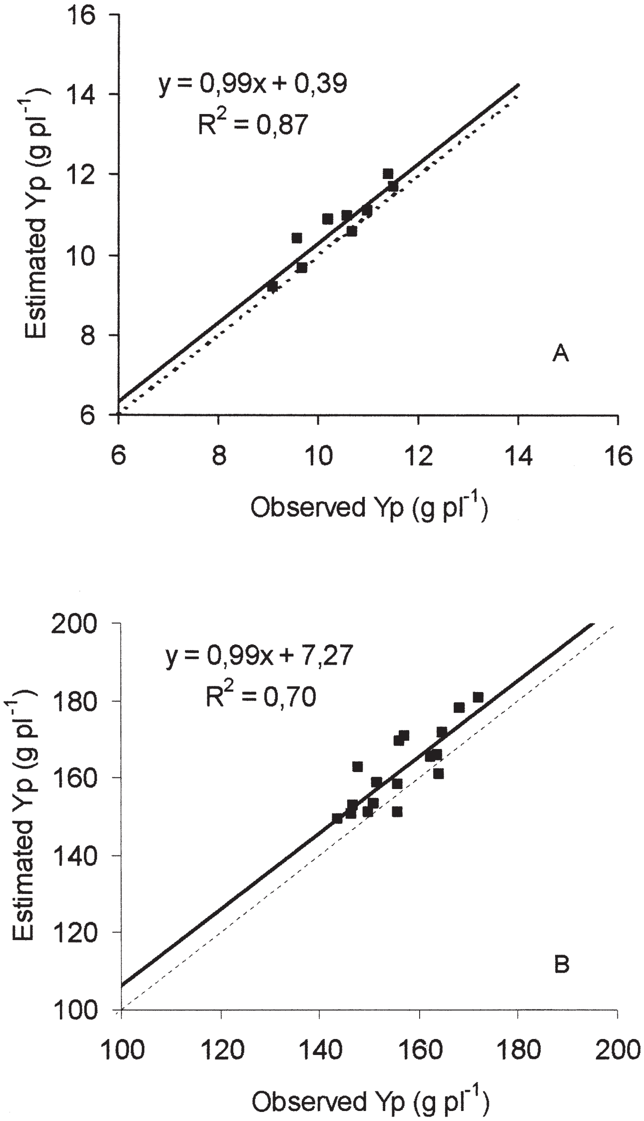

Fig. 3. Relationship between estimated and observed mean plant yield (Yp) for (A) soybean and (B) maize. The Yp values of all experimental units from Exp. 1, 2, and 4 were estimated with Eq. [4]. The linear equation fitted to the data was $y = 0.39 + 0.992x$ ($R^2 = 0.87$) for soybean and $y = 7.48 + 0.987x$ ($R^2 = 0.70$) for maize. The dotted line represents the one-to-one relationship.

Differential responses to uneven stands could also be explained by differences in vegetative plasticity among cultivars. Mean Vp of hybrids with low vegetative plasticity would be affected by unevenness in plant spacing. A reduction in average Vp from 150 to 140 g in response to an increase in uneveness would render in nonprolific M400 hybrid (Table 2, Case 4) a further 4.7% reduction in grain yield. However, this effect would depend on the specific Yp vs. Vp function of the cultivar.

DISCUSSION

Maize yield responded to uniformity in seedling emergence. Important yield decreases in response to uneven seedling emergence were also observed by Nafziger et al. (1991) and Liu et al. (2004a). Uneven plant spacing tended to result in lower maize yields. Negative effects of unevenness in plant spacing on maize yield were observed by Krall et al. (1977) and Vanderlip et al. (1988) in contrast to results reported by Erbach et al. (1972), Muldoon and Daynard (1981), and Liu et al. (2004b). In soybean, yield did not respond to increases in within-row plant spacing variation nor in seedling emergence variation as it was reported by Egli (1993a). In agreement with these findings, estimations based on Eq. [4] indicated that increases in CV for Vp did not affect soybean yield but reduced maize yield (Fig. 4).

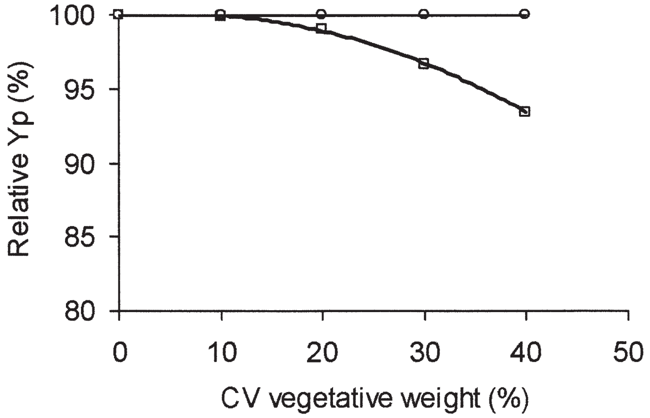

Fig. 4. Estimated relative yield per plant (Yp) as a function of percentage coefficient of variation for vegetative biomass (CV) for soybean cultivar A3901 (circles) and maize hybrid DK752 (squares). Values were estimated according to Eq. [4]. Average vegetative biomass per plant (Vp) was assumed to be 10 and 150 g plant^{-1} for soybean and maize, respectively.

Two main mechanisms explain the crop-specific responses to stand uniformity. First, increases in unevenness resulted in reductions in average Vp in maize but not in soybean. Differences in vegetative plasticity in response to resource availability per plant may contribute to explain these results. Dominant maize plants do not tiller much (Doebley et al., 1997), show low plasticity in leaf area in response to the amount of resources per plant (Williams et al., 1968; Cox, 1996; Tetio-Kagho and Gardner, 1988), and would have lower radiation use efficiency if growth is sink limited during the vegetative period. In contrast, soybean plants have high vegetative plasticity resulting from increased branching as individuals have more resources to explore (Shibles and Weber, 1966; Valentinuz, 1996; Carpenter and Board, 1997). Under nonuniform spacing between plants, maize crops usually do not achieve full light interception at the critical moments for grain yield determination whereas soybean crops do (unpublished data).

The second mechanism involved is the response of Yp to Vp (Fig. 1 and Fig. 5), which is curvilinear with a high threshold value for grain yield in maize and almost linear with no detectable threshold for grain yield in soybean. These relationships result from grain number and grain weight adjustments to the amount of resources available per plant (Andrade et al., 1999; Vega et al., 2000, 2001) and reflect the greater reproductive plasticity of indeterminate soybean compared with determinate plants (maize) with high threshold Vp for Yp and limited capacity to adjust sink size in response to resource availability (Loomis and Connor, 1996). The de-

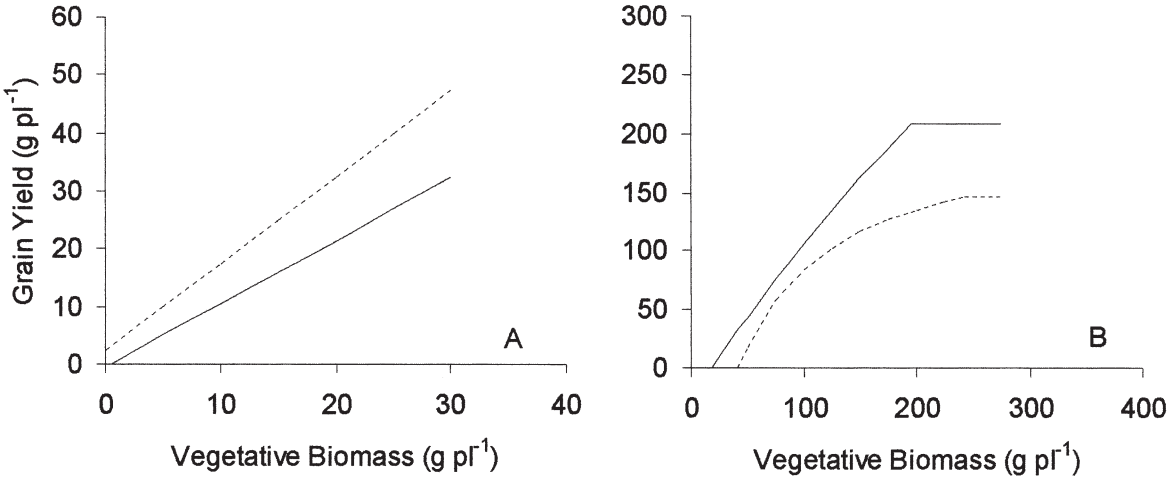

Fig. 5. Yield per plant as a function of vegetative biomass per plant for: (A) two soybean cultivars, according to Eq. [3], A3901 (solid line, $a = -0.47$, $b = 1.1$; $R^2 = 0.97$) and A3205 (broken line, $a = 2.5$, $b = 1.5$; $R^2 = 0.95$) and (B) two maize hybrids, according to Eq. [1], DK752 (solid line, $a = 1.42$, $b = 18.57$, $c = 0.0012$, and $d = 196.0$; $R^2 = 0.97$) and M400 (broken line, $a = 2.42$, $b = 41.87$, $c = 0.0116$, and $d = 241.5$; $R^2 = 0.82$).

Table 2. Estimated relative average yield per plant reduction due to an increase in percentage coefficient of variation for vegetative biomass per plant (Vp) from 0 to 35% for maize hybrids considering two different relationships between yield per plant (Yp) and Vp (hybrid DK752 or M400); mean Vp values of 150 g/plant for controls and nonuniform stands in hybrids with high vegetative plasticity or 140 g/plant for nonuniform stands in hybrids with low vegetative plasticity; and nonprolific or highly prolific hybrid. Data were computed according to Eq. [4]. Equation [1] parameters were $a = 1.42$, $b = 18.57$, $c = 0.0012$, and $d = 196.0$ for DK752 ($R^2 = 0.97$) and $a = 2.42$, $b = 41.87$, $c = 0.0116$, and $d = 241.5$ for M400 ($R^2 = 0.82$). The function to account for yield of secondary ears was Ypa = 3.01 (Vp − 193.8)/[1 + 0.023(Vp − 193.8)].

Case	Prolificacy	Vp plasticity	Uppermost ear Yp/Vp relationship	Relative yield reduction
				%
1	High	high	DK752	−0.5
2	No	high	DK752	4.9
3	No	high	M400	8.4
4	No	low	M400	13.1

crease in average Vp and the curvilinear nature of the Yp vs. Vp relationship in maize indicate that Yp increments of dominant plants do not compensate for the decrease in Yp of dominated plants. Contrarily, the lack of effect of uneven stands on Vp and the linear relationship between Yp and Vp in soybean point out the yield compensation between dominant and dominated plants.

As a result of these mechanisms, the yield loss in late-emerging plants is compensated for by increased yield of early emerging plants in soybean but not in maize. Moreover, grain yield loss of plants placed very close to their neighbors would be compensated for by the additional yield of plants that receive additional radiation in soybean but not necessarily in maize, in agreement with findings by Pommel and Bonhomme (1998). Briefly, within-row plant variability would not be detrimental to yield if there is no decrease in solar radiation interception and if vegetative and reproductive growth of uneven stands are not more sink limited than those of the uniform controls. According to the characteristics of the plants, these conditions are more likely to be met in soybean than in maize stands.

Model-derived yield of two soybean cultivars was not affected by plant unevenness. It seems, then, likely that the lack of effect of unevenness in Vp on soybean grain yield is a common response provided adapted cultivars are planted at recommended plant densities and planting dates. Late plantings without appropriate plant density adjustments would result in more response to unevenness because of the lower vegetative plasticity generally observed under these conditions (Carter and Boerma, 1979; Weaver et al., 1991). Moreover, short-season cultivars would be more responsive to uniform stands because potential vegetative weight and the capacity of the plant to explore available resources is proportional to the cultivar maturity group (Egli, 1993b).

The effect of unevenness in plant sizes on maize grain yield clearly depends on the characteristics of the hybrid. A stable hybrid would be characterized by low decreases in Vp in response to heterogeneity, low threshold Vp for prolificacy and for grain yield, and high uppermost ear plasticity. Opposite features would be found in non-stable genotypes. Tollenaar and Wu (1999) found that modern hybrids were more tolerant to plant-to-plant variability than old hybrids. A higher reproductive plasticity and lower Vp threshold for grain yield in modern hybrids (Echarte and Andrade, 2003) would explain these results.

Without appropriate plant density adjustments, short-season cultivars would be more affected by nonuniform within-row plant spacing because of the low vegetative plasticity generally observed in these hybrids (unpublished data).

Plant density and environmental conditions would affect the response of maize to uneven emergence and spacing because they affect average Vp and competition for resources that in turn result in variation in plant compensatory mechanisms, Vp reduction, and distribution. For example, at low densities, crop responses to uneven emergence are less frequent (Pommel et al., 2002) because plants do not strongly compete for resources. Contrasting environmental conditions during vegetative and reproductive growth would affect the Yp vs. Vp relationship of the cultivar and the model prediction ability. The model prediction ability would be also reduced when the assumption of a normally distributed Vp is not met (Nafziger et al., 1991). A clear example of this situation is when the crop is planted with low soil moisture and some of the seedlings emerge early and the rest later after the soil is wet by a rain. A bimodal Vp frequency distribution should be used in this case.

CONCLUSIONS

Increases in CV for Vp resulted in less grain yield in maize but not in soybean. The effect of unevenness in plant sizes on maize grain yield would depend on the characteristics of the hybrid. A stable hybrid is characterized by low decreases in Vp in response to heterogeneity, low threshold Vp for prolificacy and for grain yield, and a low curvature in the Yp/Vp relationship.

These genotypic effects would be some of the reasons for the contrasting responses of maize crops to variability in intrarow spacing reported in the literature (Erbach et al., 1972; Krall et al., 1977; Johnson and Mulvaney, 1980; Muldoon and Daynard, 1981; Liu et al., 2004b).

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