



Spatial and temporal plant-to-plant variability effects on soybean yield

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ARTICLE INFO

Keywords:

Planting quality
Crop establishment
Seed quality
Individual growth rate

ABSTRACT

Plant density and row spacing are management practices that farmers use to maximize soybean (*Glycine max* (L.) Merr.) yield. Other canopy aspects related to seedling establishment like spatial (spacing among plants) and temporal (timing of plant emergence) within-row plant-to-plant variability have received less attention. Negative yield effects of non-uniform stands have been reported for maize (*Zea mays* subsp. *Mays* L.), but it is commonly accepted that soybean plants compensate for any plant-to-plant growth difference. Planting quality is becoming relevant because small yield effects can have a high economic return due to high soybean prices and low implementation costs. The objectives were to assess the impact of non-uniform spatial and temporal seedling establishment on soybean yields and to identify putative mechanisms. Results showed that, across planting dates and plant densities, there was no yield loss due to increased spatial plant-to-plant variation in a later maturity group cultivar (MG IV), but reduced yield in an earlier one (MG III). Contrarily, non-uniform temporal distributions significantly reduced yield across cultivars. Having a poor spatial distribution had no effect on the average plant growth rate or its plant-to-plant variability. A poor temporal distribution did not affect individual average plant growth rate but variability was increased. This increased variability determined that some individuals had higher plant growth but reduced seed number because of reduced reproductive partitioning. Novel findings can be summarized as: (i) the higher relative importance of temporal vs. spatial non-uniform canopies in determining soybean yield reductions, (ii) the influence of reduced seed set at higher plant growth rates to mechanistically explain yield reductions in non-uniform temporal canopies; (iii) the concept that the yield effect of non-uniform temporal canopies cannot be overcome by increased plant densities. Future research needs to better understand the interactions between cultivar reproductive characteristics and susceptibility to non-uniform temporal canopies.

1. Introduction

Soybean is the main source of protein for animal feed worldwide, with a global production of 351 million metric tons in 2017 (Statista, 2017). Satisfying a growing population demanding more animal protein requires soybean production to increase further (Cassman, 1999). Given the lack of additional farmland, global production increases will depend on higher yields at the farm level. Maximizing yield requires optimizing several management practices. The selection of plant density is an important one since it impacts crop leaf area index needed to optimize radiation interception and crop growth (Vega et al., 2001a; Vega and Sadras, 2003; Andrade and Abbate, 2005; De Bruin and Pedersen, 2008). Once plant density is established, non-uniform seedling emergence may affect individual plant growth and can have a yield-reducing impact at the crop canopy level (Benjamin, 1990).

Spatial non-uniformity relates to plant-to-plant within-row

distribution, while temporal non-uniformity relates to timing in plant-to-plant emergence. Both components of planting quality can cause yield losses. Spatial variability is usually a consequence of non-uniform crop residue distribution (Liu et al., 2004c; Andrade and Abbate, 2005), planting system (plate or drilled) (Liu et al., 2004c; Nielsen, 1995), soil compaction (Mahdi and Hanna, 2006), and soil crusts due to heavy rain (Elmore and Abendroth, 2006; Nafziger et al., 1991). Temporal variability, and the generation of different plant cohorts, can be a consequence of delayed germination due to seed quality problems (Egli, 1993b), limited soil water availability (Mahdi and Hanna, 2006; Nafziger et al., 1991), differences in planting depth within-row (Andrade and Abbate, 2005; Liu et al., 2004b), or low soil temperature (Garcia-Huidobro et al., 1982). Expected yield penalties depend on the crop specific compensatory mechanisms.

Negative yield effects of poor seeding establishment have been widely studied in maize (Andrade and Abbate, 2005; Liu et al.,

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2004a,b,c; Vega and Sadras, 2003; Nafziger et al., 1991; Rossini et al., 2012; Tollenaar and Wu, 1999). Results indicate significant yield decreases with poor uniformity at emergence and/or uneven plant-to-plant spacing. This is related to poor reproductive plasticity in dominant plants and reductions in reproductive partitioning in dominated plants (Vega et al., 2001a; Vega and Sadras, 2003). Compared to maize, soybean plants have a higher capacity to compensate for plant-to-plant growth differences during the seed set period. This is associated with a more linear relationship between growth during this period and seed number (Jiang and Egli, 1995; Vega et al., 2001a,b). The nature of this linear relationship allows dominant plants having additional resources, due to spatial and/or temporal planting variability, to effectively use them for set seed. On the other hand, dominated soybean plants set seeds even at very limited plant growth without reductions in reproductive partitioning (Valentinuz, 1996; Carpenter and Board, 1997; Andrade and Abbate, 2005; Vega et al., 2001a,b). These features, compared to maize, determine higher soybean reproductive plasticity, making the crop less susceptible to increased plant-to-plant variability.

There are a limited number of studies evaluating yield penalties related to non-uniform soybean canopies. This can be related to smaller yield penalties expected in soybean compared to other crops like maize. However, studying this process in soybean is becoming especially relevant because even small magnitude yield effects can have a low cost-benefit ratio due to higher soybean prices and the low cost of implementing better planting techniques. Few attempts to quantify this effect are available. Stivers and Swearingin (1980) evaluated the effect of spatial distribution based on the effect of patches without plants. These authors found yield reductions between 1.1 and 15.0% due to spatial variation problems. Moore (1991) found that the negative effect of a poor spatial distribution was higher in years with lower yields, also finding a significant interaction between plant density and spatial distribution on yield. Tourino et al. (2002) found that a better spatial distribution determined less lodging probability. In terms of temporal variation, Egli (1993b) found that reductions in plant growth of dominated plants were fully compensated by the dominant ones, with no yield penalties. Finally, Andrade and Abbate (2005) evaluated both spatial and temporal variability in a single soybean genotype, planting date, and plant density, and found no yield effects. These diverse, yet scarce, findings warrant further exploration of the role of spatial and temporal variation in stand establishment on soybean yields and associated interactions with other management practices. Our working hypothesis is that more compact and short cycle modern cultivars (De Felipe et al., 2016) have less capacity for compensating spatial and temporal non-uniform canopies.

Our first objective was to assess the impact of spatial and temporal variability in soybean yield. Particularly, we were interested in understanding how planting quality issues interact with soybean maturity group, planting date, and plant density. We hypothesize that (i) uniform temporal and spatial distribution are required to achieve potential soybean yields, and (ii) the negative effect of non-uniform canopies are more pronounced in earlier maturity groups, late planted, and at low plant density. A second objective was to understand the mechanisms by which planting quality might affect soybean yield. To address this objective we evaluated the different seed number determination parameters as described in Charles-Edwards's model (Charles-Edwards, 1984).

2. Materials and methods

2.1. Experimental details and crop culture

Two field experiments were conducted at the Campo Experimental Villarino (33°1' S, 60°53' W), Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, located in Zavalla, Santa Fe, Argentina. Experiment 1 (Exp. 1) was conducted in 2012/13 and 2013/14, and experiment 2 (Exp. 2) was conducted in 2014/15. Soil type was

a silty clay loam Vertic Argiudoll, Roldán series. Plots were four rows, six meters long, and 0.52 m inter-row spacing. Seeds were inoculated at recommended rates with RizoLiq LLI® (Rizobacter Company, Argentina) containing *Bradyrhizobium japonicum* (strain E109) and an osmo-protector to sustain bacteria viability after seed pesticide application. Compatible seed insecticide and fungicide Cruiser Advanced® (Syngenta Company, Argentina) was applied at a rate of 1 cm³ seed kg⁻¹. Seed treatments were professionally applied two weeks before planting. Vigor and germination were not tested, but seed was certified-seed with professional seed treatments. Weeds were chemically controlled with recommended herbicides, and pests and diseases were controlled by spraying recommended products for the region. Soil available N (quantified as N-NO₃⁻ in the upper 60 cm depth) before planting was 41, 35, and 67 kg ha⁻¹ for 2012/13, 2013/14, and 2014/15, respectively. Extractable P (P-Bray) was 12.1, 44.1, and 5.6 mg kg⁻¹, and soil organic matter was 30.2, 28.3, and 32.2 g kg⁻¹ for 2012/13, 2013/14, and 2014/15, respectively. Plots were broadcast fertilized at planting with 120 kg ha⁻¹ mono ammonium phosphate (11-52-0 of N-P-K). Soil water at planting was gravimetrically determined at 2 m soil depth using a soil probe. Total available soil water was 282, 41 and 187 mm for growing seasons 2012/13, 2013/14, and 2014/15, respectively. Rainfall from planting to physiological maturity was 637, 650, and 438 mm for the three years. Rainfall distribution during each growing season is presented in Fig. 1. For the three growing seasons, rainfall plus initial soil water was more than 600 mm. According to Grassini et al. (2015), water availability of 600 mm sets a yield potential of approximately 5000 kg ha⁻¹.

2.2. Experimental design and treatments

Both experiments had a randomized complete block design with five (Exp. 1) and four (Exp. 2) replicates. Early and late planting dates for Exp. 1 were November 13 and December 27 for the 2012/13 growing season, and December 2 and December 28 for the 2013/14 season. Experiment 2 was conducted on a single planting date (December 11). Plots were planted with a no-till cone planter at 2–3 cm planting depth, at 50 seeds m⁻², and final plant density was adjusted between 6 to 8 days after emergence by hand thinning (Fehr and Caviness, 1977). Since the plant density needed to maximize yield is strongly affected by planting date, low and high plant density treatments were determined relative to the planting date (Lawn and James, 2011; Boquet, 1999). The low plant density treatment was 10 plants m⁻² for the early planting date and 20 plants m⁻² for the late planting date. The high plant density was 20 plants m⁻² for the early planting date and 40 plants m⁻² for the later one. Even though plant density is not balanced, the plant density levels (low and high) are balanced across planting dates. Two cultivars belonging to different maturity groups (MG) were evaluated at both experiments. Cultivar SPS3 × 1 is MG III, and SPS4 × 99 is MG IV. According to seed company information, cultivar

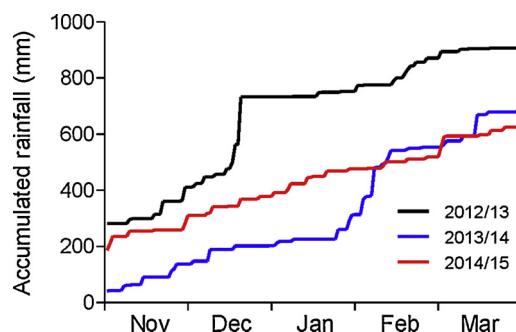


Fig. 1. Accumulated rainfall during the 2012/13, 2013/14, and 2014/15 growing seasons at Campo Experimental Villarino experimental site. Soil water before planting is indicated by the y-intercept.

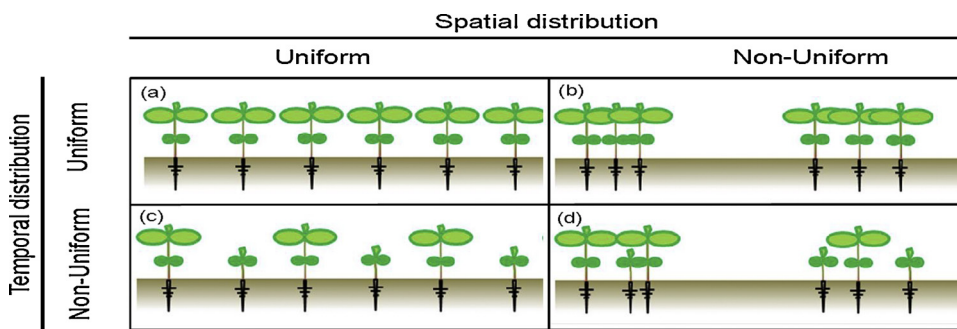


Fig. 2. Graphical representation of spatial and temporal treatments affecting the plant-to-plant variability within stands. Fig. 2a represents the uniform spatial and temporal plant-to-plant distribution, Fig. 2b the non-uniform spatial and uniform temporal plant to plant distribution, Fig. 2c the uniform spatial and non-uniform temporal plant-to-plant distribution, and Fig. 2d the non-uniform spatial and temporal distribution. These four treatments were tested with different genotypes, plant densities, and planting dates for two years.

SPS3 \times 1 is indeterminate, average cycle is 117 days to R8, has low branching ability, intermediate lodging susceptibility, and optimum planting dates spans from early October to early November. Cultivar SPS4 \times 99 is also indeterminate, average cycle is 144 days to R8, has high branching ability, low lodging susceptibility, and recommended planting date extends from mid-October to December (<https://www.syngenta.com.ar/soja>, accessed on November 2017).

The impact of planting quality on yield was assessed by a series of manipulative treatments modifying the spatial and temporal pattern of seedling establishment: (i) uniform control, (ii) non-uniform within-row plant-to-plant spacing (spatial distribution treatment), (iii) non-uniform plant-to-plant temporal seedling emergence (temporal distribution treatment) and (iv) a combination of both treatments. Fig. 2 provides a graphic representation of the four treatments. The uniform control treatment was obtained after hand thinning to targeted plant density using sticks with marks for guidance. The spatial distribution treatment was obtained by hand thinning at the prescribed densities but leaving groups of 3–4 plants spaced less than 2 cm. The temporal distribution treatment was obtained by first thinning the plots (uniform for the uniform control and non-uniform for the spatial distribution treatment). Then soon after V1, half the seedlings were removed alternately and a seed was sown in the same position where the seedling was removed. This generated a second cohort of seedling emergence, creating the temporal distribution treatment. Treatments were applied to the entire plots. Irrigation (10 mm) was applied to the experiments to facilitate germination of the replanted seeds.

In summary, experiments involved the factorial combination of planting date (early and late, only Exp. 1), cultivar (MG III and MG IV), plant density (low and high), spatial variation (control and non-uniform) and temporal variation (control and non-uniform).

2.3. Response variables

2.3.1. Variables for experiments 1 and 2

The within-row distance between consecutive individual plants was measured at V5 in each plot along four meters of the two central rows. The mean and standard deviation of the distance among plants was calculated. The magnitude of spatial variation in seedling establishment was then estimated as the coefficient of variation of the distance among plants (spatial distribution CV, standard deviation mean⁻¹ \times 100).

Number of nodes below the last one with a fully developed leaf was counted five weeks after planting on each plant along four meters of the two central rows. The mean number of nodes per plant and the standard deviation were calculated. The magnitude of temporal variation in seedling emergence was then estimated by the coefficient of variation of nodes per plant (temporal distribution CV, standard deviation mean⁻¹ \times 100).

Plants were counted at maturity in each plot along four meters of the two central rows (4.16 m²). Plants in those areas were hand clipped and threshed with a stationary harvester. Seeds were weighed, and the weight of a 200 seed sub-sample was used to calculate individual seed dry weight in each plot. Seed yield is reported with zero

moisture. Seed number per unit land area was calculated dividing yield over the individual seed weight.

2.3.2. Variables for experiment 2

In Exp. 2 an allometric approximation (Vega et al., 2001a) was followed to estimate the average and coefficient of variation of: (i) individual plant growth rate during the seed number determination period (from R1 to R5), (ii) biomass partitioning to reproductive structures during this same period, and (iii) seed set efficiency, as defined in the Charles Edwards's model (1986) and modified in Rotundo et al. (2012). Nine plants per plot were tagged at V3 for building allometric relationships to estimate total biomass at R1, R3, and R5. On these tagged plants, stem diameter at soil level was measured using a caliper at R1, R3, and R5. Growth stages were determined on a cultivar base. After each measurement, three plants were hand clipped, dried in an air forced oven for more than 96 h at 65 °C, and weighed. For the three plants measured at R5, pods longer than 3 cm were counted and separated, leaving separated reproductive (pod + seeds) and vegetative biomass samples per plant. Since these were destructive measurements, plants were tagged elsewhere but in the two central rows avoiding the four meters where R7 plants would be harvested for final yield. Allometric relationships between stem diameter and total aboveground biomass, and between number of pods and reproductive biomass (only for R5 samples), were constructed for each developmental stage and cultivar using the four replications (96 plants per genotype at each developmental stage). Simultaneously, the stem diameter at R1, R3, and R5, and the pod number per plant at R5 were measured on 30 consecutive tagged plants per plot at the two central rows. The allometric relationships generated with the destructive measurements were used to estimate total biomass (and reproductive biomass at R5) on these 30 plants per plot.

Individual plant growth rate (g plant⁻¹ day⁻¹) during the seed set period was calculated as the linear slope of the relationship between estimated plant biomass (at R1, R3, and R5) and days. Biomass partitioning to reproductive structures (Part_{R1-R5}) was calculated as the ratio between reproductive biomass at R5 and individual plant growth rate. Finally, seed set efficiency (seed g biomass at R5⁻¹) was calculated as the ratio between seed number at R7 and the accumulated reproductive biomass at R5. Determining reproductive growth (and therefore seed set efficiency) is sensible to variation in sampling date. However, despite being sensible to sampling date it was possible to detect variation in seed set efficiency across species (Vega et al., 2001a,b), and within species (Rotundo et al., 2012). Each replicate was sampled at R5 date.

These plants were individually harvested at R7 and seed number and total seed weight was determined per plant. After harvesting these individual plants, the remaining of the sampling area was hand clipped and threshed with a static harvester. Seed yield and numerical components (seed number and individual seed weight) were determined. The seed weight of the 30 individual plants was added to the sampling area to correctly estimate yield on an area basis.

2.4. Statistical analysis

Data on seed yield, numerical yield components (seed number and individual seed weight), and the coefficient of variation for the spatial and temporal distributions from Exps. 1 and 2 were analyzed using proc Mixed from SAS (1999). The model included years (only Exp. 1) and blocks as random factors, while planting date (only Exp. 1), plant density, cultivar, temporal variation, spatial variation, and all the interactions were considered fixed factors. For Exp. 2 the same statistical model was used for analyzing the mean and coefficient of variation of individual plant growth rate, reproductive biomass partitioning, and seed set efficiency. Year was considered random because it is a factor not controlled by us, and therefore there is no interest in assessing a fixed effect on a factor level that is not possible to replicate. On the other hand, Exp. 1 was a large experiment with five fixed factors with several levels. Adding year as another factor would have complicated results interpretation. Fisher's protected LSD (least significant difference) was calculated for significant ($P < 0.05$) effects. Only those experimental sources with significant effects at $P < 0.05$ are reported in the results section. The complete analysis of variance for each variable is included as supplemental information.

A regression analysis was conducted between (i) seed number per plant and individual plant growth rate from R1 to R5, (ii) reproductive biomass at R5 and plant growth rate from R1 to R5, and (iii) seed number per plant and reproductive biomass per plant at R5 using a hyperbolic model (Vega et al., 2001a):

$$y = \frac{\alpha(x - x_0)}{1 + \beta(x - x_0)} \quad \text{for } x > x_0 \quad (1)$$

where α is the initial slope of the relationship, x_0 is the threshold for $y > 0$, and β is the curvature of the relationship at high x values. Both relationships were fitted individually for each cultivar. This hyperbolic model was compared against a simpler straight linear model using GraphPad Prism 6.00 (GraphPad Software, La Jolla California USA) using an AIC approximation (Akaike, 1998) corrected for finite samples (AICc; Hurchiv and Tsai, 1989.). The difference between the two AICc values (AICc of the linear model minus the AICc of the hyperbolic model) is reported. If the difference is positive, the hyperbolic model is preferred. If negative, the straight linear model is used.

3. Results

3.1. Observed planting quality and final plant density (Exps. 1 and 2)

The temporal distribution CV was affected by the temporal variation treatment in both experiments (Tables 1 and 2). On average across treatments, the temporal non-uniform distribution CV was twice the temporal uniform control ($P < 0.05$). For Exp. 1, the temporal distribution CV showed a significant interaction between planting date and cultivar ($P < 0.05$). The later planting date increased the temporal CV, and this effect was more pronounced for SPS4 \times 99 than for SPS3 \times 1. The frequency distribution of the number of nodes across plants within the canopy is presented in Fig. 3 and visually describes the magnitude of the temporal variation in emergence across experiments, planting dates, and plant densities.

The spatial variation treatment increased the spatial CV in both experiments (Tables 1 and 2). Overall, the spatial CV increased 90% when compared to the uniform control. An interaction between plant density and spatial distribution treatment was observed for Exp. 1 (Table 1); the spatial CV of the non-uniform spatial distribution treatment increased more at the lower plant density (+95%) than at the higher one (+67%). A significant interaction was observed between the spatial and the temporal distribution treatments. The effect of the spatial distribution treatment on the spatial CV was higher in the uniform temporal control (+100%) than in the non-uniform temporal (+62%) treatment (Table 1). In Exp. 2, the spatial CV was different

between cultivars as cultivar SPS4 \times 99 had a greater spatial CV than SPS3 \times 1 (Table 2). The frequency distribution of the within-row distance between consecutive plants, as a measure of the spatial variation, is presented in Fig. 3. The non-uniform spatial treatment increased the number of plants with a reduced distance between plants when compared to the uniform spatial treatment.

Plant density was effectively modified by the plant density treatments. In the first planting date of Exp. 1 the plant density difference between the low and high density treatments was $\sim 60\%$, while for the late planting date it was increased by $\sim 45\%$ (planting date \times plant density significant interaction, $P < 0.05$, Table 1). In Exp. 2 plant density was 83% greater in the high plant density treatment when compared to the lower one (Table 2). In Exp. 1 the temporal manipulative treatment slightly affected plant density. The uniform control was reduced 3 plants m^{-2} compared to the non-uniform temporal variation treatment (Table 2). This effect was not observed in Exp. 2. The spatial distribution treatment did not affect plant density.

In brief, our manipulative treatments effectively affected the temporal and spatial plant-to-plant variability within canopies. Although the final plant densities were slightly different than the targeted densities our low and high density treatments were always different.

3.2. Planting quality and soybean yield and numerical components (Exps. 1 and 2)

Soybean yield in Exp. 1 was greater at the earlier planting date when compared to the later one ($P < 0.05$, Table 3). On average across planting dates, cultivar SPS4 \times 99 out-yielded SPS3 \times 1 by $\sim 14\%$ ($P < 0.05$, Table 3). This yield advantage was higher in the early (+518 $kg\ ha^{-1}$) compared to the late (+305 $kg\ ha^{-1}$) planting date (planting date \times cultivar interaction, $P < 0.05$, Table 3). In the late planting date of Exp. 2 there was no significant yield difference between cultivars (Table 4).

Increased plant density had a small positive effect on yield (+80 $kg\ ha^{-1}$) across planting dates and cultivars ($P < 0.05$, Table 3). However, this effect was larger in Exp. 2, where the higher plant density produced a yield almost 200 $kg\ ha^{-1}$ greater than the low plant density (Table 4).

Lower soybean yield in late planting was a consequence of reduced seed number and seed size ($P < 0.05$, Table 3). Superior yield of cultivar SPS4 \times 99, when compared to SPS3 \times 1, was associated with greater seed number ($P < 0.05$, Table 3). The reduced seed size associated with later plantings was more pronounced for SPS4 \times 99 than for SPS3 \times 1 (planting date \times cultivar interaction, $P < 0.05$, Table 3). The positive yield effect from increased plant density was associated with more seeds in Exp. 2 (Table 4).

Canopy planting quality changes generated several significant yield effects. There was a significant cultivar \times spatial treatment interaction in Exp. 1 ($P < 0.05$, Table 3). This interaction showed that, across planting dates and plant densities, there was no yield effect from increased plant-to-plant spatial variation for cultivar SPS4 \times 99, but a non-uniform spatial distribution caused a significant yield reduction in SPS3 \times 1. This yield reduction was $\sim 6\%$ relative to the uniform control. The negative yield effect of increased plant-to-plant spatial variation observed in Exp. 1 was not detected in Exp. 2. No yield effect was observed in Exp. 2 for any genotype due to non-uniform spatial distribution.

Non-uniform plant-to-plant temporal distributions significantly affected yield ($P < 0.05$, Table 1). The yield reduction caused by a non-uniform temporal distribution was observed in both experiments, and across planting dates, plant densities, and cultivars. The magnitude of this reduction was 7 and 8% relative to the uniform control for Exps. 1 and 2, respectively (Tables 3 and 4).

Although only a trend in many cases, lower seed number per unit land area helped explain yield reductions caused by non-uniform spatial and temporal distributions. No effects were observed over

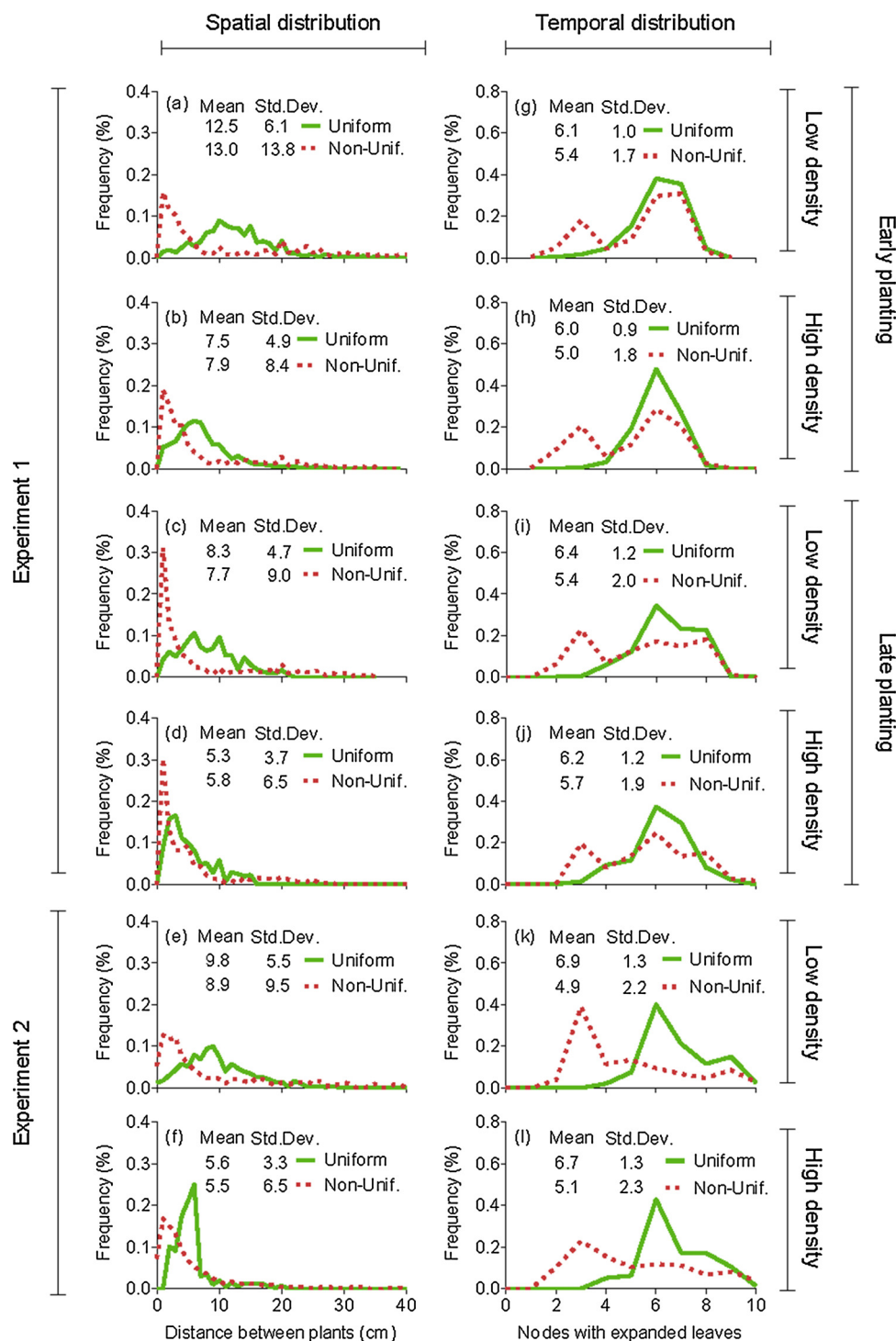


Fig. 3. Frequency distribution of distance among individual plants and number of nodes per plant, as an indicator of spatial and temporal variation of soybean seedling establishment, respectively. The full green line represents the uniform treatment while the broken red line represents the non-uniform treatment as presented in Fig. 2. Panels correspond to different experiments (Exps. 1 and 2), planting dates (early and late), and plant densities (high and low). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

individual seed size.

3.3. Individual plant growth rate, biomass partitioning, and seed set efficiency (Exp. 2)

In all cases r^2 for the allometric models used to estimate individual plant parameters were higher than 0.80 ($P < 0.001$). Plant growth rate was different across cultivars and plant densities (Table 5). Overall,

cultivar SPS3 × 1 had a significantly greater plant growth rate than cultivar SPS4 × 99. As expected, the lower plant density increased individual plant growth rate when compared to the higher plant density. The CV of individual plant growth was affected by the temporal variation treatment (Table 5). The non-uniform temporal distribution treatment almost doubled the CV of plant growth rate compared to the uniform control (Table 5). This effect was less pronounced for SPS3 × 1 (71%) than for SPS4 × 99 (96%), as shown by the significant cultivar ×

Table 1

Observed coefficient of variation (CV) of plant-to-plant differences in temporal and spatial distribution and final plant density affected by planting date, plant density, cultivar, and spatial and temporal distribution in Exp. 1. Only significant ($P < 0.05$) effects and interactions are reported. Complete ANOVA is described in Supplemental Table S1. Different letters indicate significant differences within each source of variation (L.S.D. test).

Source of variation		CV temporal distribution (%)	CV spatial distribution (%)	Plant density at harvest ($\# \text{ m}^{-2}$)	
Planting date	Early	23.4 b	79.3 b	20.9 b	
	Late	34.5 a	86.4 a	30.4 a	
Plant density	High	28.7	84.7 a	30.8 a	
	Low	29.3	81.0 b	20.5 b	
Planting date x Plant density	Early	High	24.0	82.1	25.7 b
		Low	22.9	76.5	16.1 c
	Late	High	33.3	87.4	35.9 a
		Low	35.7	85.4	24.9 b
Planting date x Cultivar	Early	SPS3 \times 1	24.2 c	80.7	21.2
		SPS4 \times 99	22.7 c	77.9	20.6
	Late	SPS3 \times 1	31.8 b	89.0	29.7
		SPS4 \times 99	37.2 a	83.8	31.1
Spatial distribution	Uniform _{sp}	29.1	59.1 b	25.9	
	Non-uniform _{sp}	28.9	106.6 a	25.4	
Plant density x Spatial distribution	High	Uniform _{sp}	28.7	63.4 b	30.9
		Non-uniform _{sp}	28.7	106.0 a	30.7
	Low	Uniform _{sp}	29.5	54.8 b	21.0
		Non-uniform _{sp}	29.1	107.1 a	20.0
Temporal distribution	Uniform _{te}	19.2 b	84.9 a	27.0 a	
	Non-uniform _{te}	38.7 a	80.8 b	24.3 b	
Spatial distribution x Temporal distribution	Uniform _{sp}	Uniform _{te}	19.2	56.4 b	27.6
		Non-uniform _{te}	39.0	61.8 b	24.3
	Non-uniform _{sp}	Uniform _{te}	19.3	113.3 a	26.5
		Non-uniform _{te}	38.5	99.8 a	24.2
Analysis of variance		F Value	F Value	F Value	
Planting date		12.6**	27.6***	61.9***	
Plant density		0.4 ^{n.s.}	5.1*	244.7***	
Planting date x Plant density		3.0 ^{n.s.}	1.2 ^{n.s.}	6.0*	
Planting date x Cultivar		11.5**	0.5 ^{n.s.}	3.5 ^{n.s.}	
Spatial distribution		0.1 ^{n.s.}	806.1***	1.2 ^{n.s.}	
Plant density x Spatial distribution		0.0 ^{n.s.}	8.4**	0.5 ^{n.s.}	
Temporal distribution		357.4***	6.0*	26.6***	
Spatial distribution x Temporal distribution		0.1 ^{n.s.}	32.1***	0.8 ^{n.s.}	

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; n.s. not significant at $P \geq 0.05$.

temporal distribution interaction ($P < 0.05$).

Biomass reproductive partitioning was only affected by the cultivar treatment (Table 5). Overall, cultivar SPS4 \times 99 partitioned more biomass to reproductive structures during the seed set period than SPS3 \times 1. Interestingly, the CV of biomass partitioning during this period was affected by the temporal distribution treatment (Table 5). The non-uniform temporal treatment showed more variability in partitioning than the uniform temporal distribution treatment (40 vs 53%, for uniform and non-uniform temporal distribution, respectively). Biomass partitioning to the reproductive structures was not affected by plant density but the increased plant density coincided with an increased partitioning CV ($P < 0.05$, Table 5). This effect was more pronounced for SPS3 \times 1 than for SPS4 \times 99, as shown by the cultivar \times plant density interaction ($P < 0.05$, Table 5). The mean and variation coefficient of seed set efficiency were not affected by any of the evaluated experimental factors (Table 5).

The relationship between seed number per plant and plant growth rate was more adequately described by a hyperbolic model than by a linear model (Fig. 4a, Table 6). For both cultivars the minimum amount of plant growth to set one seed (x_0) was not different from zero. The initial slope of the relationship (α) was greater for the cultivar SPS4 \times 99 (177 seeds per unit plant growth) compared to SPS3 \times 1 (141 seeds per unit plant growth) (Fig. 4a, Table 6). The degree of curvature (β) was greater for the cultivar SPS3 \times 1 than for the cultivar SPS4 \times 99.

The relationship between seed number per plant and plant growth rate was similar to that observed between reproductive biomass and plant growth rate. A hyperbolic model described the relationship between plant growth rate and reproductive biomass at R5 (Fig. 4b, Table 6). Model parameters for this relationship were unique to each cultivar (Table 6). Cultivar SPS4 \times 99 had a greater initial slope (α) and more curvature (β) than SPS3 \times 1. For both cultivars the minimum amount of individual plant growth rate for any reproductive biomass accumulation was not different from zero as denoted by the value of the x_0 parameter.

The relationship between seed number per plant and reproductive biomass at R5 was also different between cultivars (Fig. 4c, Table 6). For cultivar SPS3 \times 1 the relationship was hyperbolic, while for SPS4 \times 99 it was linear (model selections based on AIC reductions). For both cultivars, there was no minimum amount of reproductive biomass to set seeds, as shown by the x_0 parameter not different from zero (Table 6). These results (Fig. 4, Table 6) showed that large plant-to-plant growth differences within the canopy will not fully compensate for each other in terms of maintaining seed set.

4. Discussion

Crop management practices associated to planting date, plant density, and cultivar effects yielded the generally expected outcomes. Later plantings had reduced seed yield. Reductions in soybean yield

Table 2

Observed coefficient of variation (CV) of plant-to-plant differences in temporal and spatial distribution and final plant density as affected by planting date, plant density, cultivar, and spatial and temporal distribution in Exp. 2. Only significant ($P < 0.05$) effects and interactions are reported. Complete ANOVA is shown in Supplemental Table S2. Different letters indicate significant differences within each source of variation (L.S.D. test).

Source of variation		CV temporal distribution (%)	CV spatial distribution (%)	Plant density at harvest ($\# \text{ m}^{-2}$)
Cultivar	SPS3 \times 1	31.3	75.3 b	26.7
	SPS4 \times 99	33.2	96.9 a	27.9
Plant density	High	31.7	88.1	35.4 a
	Low	32.7	84.2	19.3 b
Spatial distribution	Uniform _{sp}	32.0	56.0 a	27.3
	Non-uniform _{sp}	32.4	116.3 b	27.3
Temporal distribution	Uniform _{Te}	18.8 b	88.7	27.9
	Non-uniform _{Te}	43.0 a	84.1	26.9
Analysis of variance		F Value	F Value	F Value
Cultivar		0.2 ^{n.s.}	12.1**	0.9 ^{n.s.}
Plant density		0.4 ^{n.s.}	0.1 ^{n.s.}	479.1***
Spatial distribution		0.0 ^{n.s.}	98.2***	0.1 ^{n.s.}
Temporal distribution		75.5***	0.9 ^{n.s.}	2.5 ^{n.s.}

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; n.s. not significant at $P \leq 0.05$.

associated with late planting dates and shorter maturity groups are usually explained in terms of shortened total cycle duration and reduced solar radiation capture (Egli et al., 1987; Salmerón et al., 2015). The effect of late planting was more pronounced for the shorter maturity group cultivar compared to the longer one as expected due to the longer vegetative period for longer season maturity groups (Egli 1993a). Overall, there was a yield response to increased plant density in both experiments and no significant interaction between planting date and plant density was observed. Lack of an interaction was expected

because the low and high plant density treatments were determined relative to the specific planting date.

Temporal variation in seeding establishment had larger yield effects than spatial variations across plants within the canopy. Non-uniform temporal distributions impacted yield in both experiments and across all treatments. Spatial variation yield effects were only observed for the earlier cultivar SPS3 \times 1 in Exp. 1. Stivers and Swearingin (1980) showed the effect of spatial plant distribution on soybean yield interacts with cultivar cycle duration. Longer maturity groups were less

Table 3

Soybean yield and its numerical components (seed number and individual seed weight) as affected by planting date, plant density, cultivar, and spatial and temporal distribution treatments in Exp. 1. Only significant ($P < 0.05$) effects and interactions are reported. Complete ANOVA is described in Supplemental Table S3. Different letters indicate significant differences within each source of variation (L.S.D. test).

Source of variation		Seed yield (kg ha^{-1})	Seed number ($\# \text{ m}^{-2}$)	Seed weight (mg seed^{-1})	
Planting date	Early	3707 a	2272 a	162 a	
	Late	2615 b	2023 b	131 b	
Plant density	High	3202 a	2172	147	
	Low	3120 b	2122	147	
Cultivar	SPS3 \times 1	2958 b	1976 b	149 a	
	SPS4 \times 99	3364 a	2319 a	144 b	
Planting date x Cultivar	Early	SPS3 \times 1	3451 b	2121	163 a
		SPS4 \times 99	3963 a	2422	161 a
	Late	SPS3 \times 1	2463 d	1831	136 b
		SPS4 \times 99	2767 c	2215	126 c
Cultivar x Spatial	SPS3 \times 1	Uniform _{sp}	3047 b	2030	150
		Non-uniform _{sp}	2867 c	1923	149
	SPS4 \times 99	Uniform _{sp}	3348 a	2317	144
		Non-uniform _{sp}	3382 a	2321	144
Temporal distribution	Uniform _{Te}	3264 a	2216 a	147	
	Non-uniform _{Te}	3058 b	2079 b	146	
Analysis of variance		F Value	F Value	F Value	
Planting date		109.9***	51.8***	43.1***	
Plant density		3.9*	1.9 ^{n.s.}	0.1 ^{n.s.}	
Planting date x Plant density		1.7 ^{n.s.}	4.5*	1.4 ^{n.s.}	
Cultivar		98.4***	88.8***	21.1***	
Planting date x Cultivar		6.4*	1.3 ^{n.s.}	13.2***	
Cultivar x Spatial		6.8*	2.3 ^{n.s.}	0.3 ^{n.s.}	
Temporal		24.8***	15.4***	0.8 ^{n.s.}	

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; n.s. not significant at $P \geq 0.05$.

Table 4

Soybean yield and numerical components (seed number and individual seed dry weight) as affected by planting date, plant density, cultivar, and spatial and temporal distributions in Exp. 2. Only significant ($P < 0.05$) effects and interactions are reported. Complete ANOVA is described in Supplemental Table S4. Different letters indicate significant differences within each source of variation (L.S.D. test).

Source of variation		Seed yield (kg ha ⁻¹)	Seed number (# m ⁻²)	Seed weight (mg seed ⁻¹)
Cultivar	SPS3 × 1	3517	2054	182 a
	SPS4 × 99	3443	1930	167 b
Plant density	High	4074 a	2309 a	177
	Low	2887 b	1675 b	172
Temporal distribution	Uniform _{Te}	3625 a	2057	176
	Non-uniform _{Te}	3365 b	1940	173
Spatial distribution	Uniform _{sp}	3433	1964	174
	Non-uniform _{sp}	3527	2019	175
Analysis of variance		F Value	F Value	F Value
Cultivar		0.5 ^{n.s.}	2.5 ^{n.s.}	66.7 ^{***}
Plant density		71.2 ^{***}	76.7 ^{***}	5.2 [*]
Temporal distribution		3.9 [*]	2.4 ^{n.s.}	3.7 ^{n.s.}

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; n.s. not significant at $P \leq 0.05$.

susceptible to non-uniform spatial distribution when compared with earlier maturity group cultivars. In general, longer maturity groups are associated with longer vegetative period and larger leaf area index compared to earlier cultivars (Egli, 1993a; Jiang and Egli, 1995; Santachiara et al., 2017). This allows longer maturity group cultivars to better compensate spatial non-uniform canopies compared to earlier maturity group cultivars.

Our measurements at the individual plant level helped explain the negative effect of non-uniform temporal canopies. Our results showed a hyperbolic relationship between seed number and plant growth rate during the seed set period. Although several studies have shown a linear relationship (i.e., Jiang and Egli 1995), others have already shown a more curved response (Vega et al., 2001a). This non-linear relationship between seed number and plant growth rate from R1 to R5 is explained by reductions in the proportion of total crop biomass that is partitioned to reproductive structures at high plant growth rates. Although our results showed that temporal distribution did not affect average canopy plant growth rate, the plant-to-plant coefficient of variation of plant growth rate rose from ~50 to 100% for uniform and non-uniform temporal distributions, respectively. This increased variability is determining there are some individuals at the tail of the distribution with increased plant growth but reduced seed set. This reflects that increased growth for dominant plants is not fully translating into more yield because of reductions in seed number per unit of plant growth. This effect of reduced seed numbers at high plant growth was also reported for other crop species like maize and sunflower (Vega et al., 2001a,b). These species have more pronounced restrictions to seed set at high crop growth rates due to morphological limitations of ear or capitulum size for maize and sunflower, respectively. In the case of soybean, there is a limitation for setting seeds at high crop growth rates, evidenced by the curvilinear relationship between seed number and crop growth, but this limitation is significantly lower when compared to these other crops.

Finding a curvilinear relationship between seed number and plant growth rate has strong implications beyond the scope of our particular study. Predicting seed number has been a long term goal of simulation models, since seed number is strongly associated to seed yield (Ritchie and Wei 2000). Attempts to predict cultivar seed number differences are traditionally based on assuming a linear relationship between seed number and crop growth rate (Rotundo et al., 2012). There are several

dynamic simulation models for soybean predicting seed number as a function of growth, reproductive partitioning, and seed set efficiency (Setiyono et al., 2010; Brisson et al., 2003). These models assume a constant seed set per unit of plant growth, based on the expected linear relationship between seed number and crop growth rate. This will result in seed number overestimations at high crop growth rates under current modeling approximations. The curvilinear nature found in our study needs to be further evaluated to determine whether current approximations for estimating soybean seed number requires revision.

The relationship between seed number and plant growth rate described in Fig. 4a could also predict a yield reduction associated with increased plant-to-plant variability in plant growth rate in spatial non-uniform canopies. However, as shown in Table 5, the spatial non-uniform treatment did not modify the average plant growth rate or the variation coefficient of plant growth rate. This lack of spatial non-uniform planting yield effect is consistent with previous studies in maize showing that, if plants emerge at the same time, spatial distribution changes create minor yield reductions (Liu et al., 2004a; Liu et al., 2004b). In crops like maize and sunflower neighboring plants accommodate leaves to avoid self-shading (Maddoni et al., 2002; López Pereira et al., 2017). This mechanism is expected to reduce light competition in plants that are too close. The existence of similar mechanisms in soybean is unknown. However, there is evidence showing shade avoidance mechanisms in soybean leaves associated to R:FR light increases (Green-Tracewicz et al., 2011). Modifying this mechanism can help reduce the impact of plant-to-plant competition in non-uniform spatial canopies.

Observed yield effects were ~200 kg ha⁻¹ for the temporal effect in Exp. 1, ~180 kg ha⁻¹ for the spatial effect in SPS3 × 1 in Exp. 1, and ~260 kg ha⁻¹ for the temporal effect in Exp. 2. Even though there was a statistically significant reduction in 3 pl m⁻² in plant density for the temporal treatment, this difference was too small for having any relevant yield impact. This 3 pl m⁻² difference cannot be confounded with the temporal yield effect. A question underlying this work was to determine whether the yield effects associated with non-uniform plant distributions were economically relevant. In our work, the average yield response was ~200 kg ha⁻¹ and two factors need to be considered to determine the agronomic and economic relevance. First, an improved planting quality can be attained by practices that have negligible costs. For example, planting with adequate soil moisture, at

Table 5
Average and coefficient of variation (CV) of individual plant growth rate from R1 to R5, reproductive biomass partitioned to reproductive structures at R5, and seed set efficiency per unit of accumulated reproductive biomass as affected by planting date, plant density, cultivar, and spatial and temporal distribution treatments in Exp. 2. Only significant ($P < 0.05$) effects and interactions are reported. Complete ANOVA is shown in Supplemental Table S5. Different letters indicate significant different (L.S.D. test).

Source of variation	Plant growth rate (g pl ⁻¹ d ⁻¹)	CV plant growth rate (%)	Reprod. partitioning (g (g pl ⁻¹ d ⁻¹) ⁻¹)	CV reprod. partitioning (%)	Seed set efficiency (seed g ⁻¹)	CV seed set efficiency (%)
Cultivar	0.76 a 0.59 b	70.6 80.2	10.0 b 13.2 a	49.0 45.1	12.7 10.0	8.2 7.1
Plant density	0.49 b 0.86 a	79.6 71.2	11.8 11.5	55.0 a 39.1 b	11.4 11.4	8.0 7.3
Temporal distribution	0.72 0.64	51.4 b 94.6 a	12.0 11.4	39.7 b 52.9 a	11.3 11.5	6.2 8.9
Cultivar x Plant density	High Low	0.55 0.98	10.4 9.7	61.0 a 36.9 b	12.9 12.5	9.2 7.3
Cultivar x Temporal distribution	High Low	0.44 0.74	13.3 13.2	49.0 ab 41.3 b	9.8 10.3	6.9 7.4
Cultivar x Temporal distribution	Uniform _{Te} Non-uniform _{Te}	0.75 a 0.78 a	10.1 10.0	43.4 53.4	12.4 13.0	7.1 9.2
Cultivar x Temporal distribution	Uniform _{Te} Non-uniform _{Te}	0.70 a 0.50 b	13.9 12.7	36.0 52.4	10.2 9.9	5.3 8.6
Analysis of variance	F Value	F Value	F Value	F Value	F Value	F Value
Cultivar	15.3**	4.4 ^{n.s.}	30.3***	1.7 ^{n.s.}	2.0 ^{n.s.}	0.2 ^{n.s.}
Plant density	80.3***	4.3 ^{n.s.}	0.5 ^{n.s.}	7.9*	0.1 ^{n.s.}	0.2 ^{n.s.}
Temporal distribution	3.8 ^{n.s.}	192.4***	1.3 ^{n.s.}	5.5*	0.2 ^{n.s.}	1.5 ^{n.s.}
Cultivar x Plant density	3.2 ^{n.s.}	8.9**	0.6 ^{n.s.}	5.0*	0.0 ^{n.s.}	0.1 ^{n.s.}
Cultivar x Temporal distribution	9.0 ^{n.s.}	8.1*	0.7 ^{n.s.}	0.5 ^{n.s.}	0.1 ^{n.s.}	0.1 ^{n.s.}

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; n.s. not significant at $P \leq 0.05$.

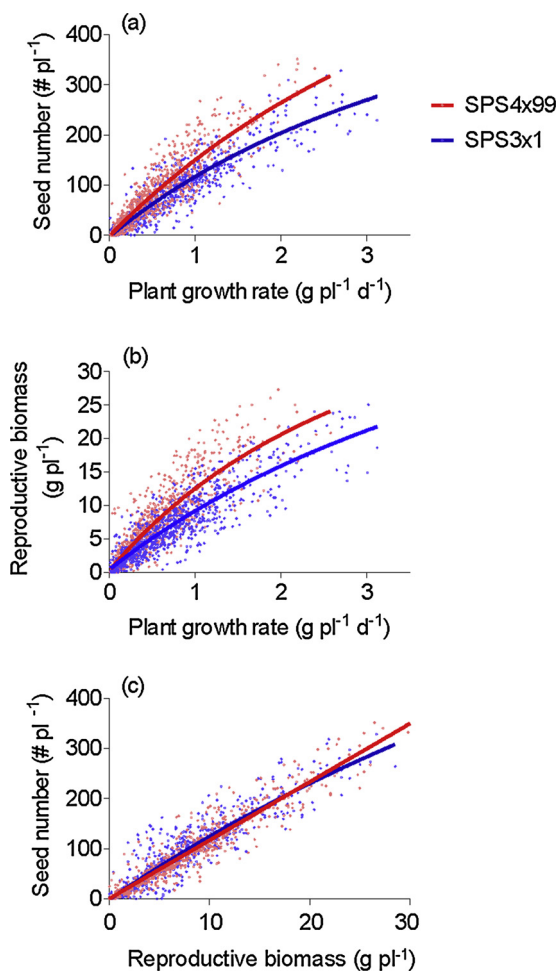


Fig. 4. Relationship between (a) seed number per plant and plant growth rate from R1 to R5, (b) reproductive biomass at R5 and plant growth rate from R1 to R5, and (c) seed number per plant and reproductive biomass at R5. Genotypes SPS4 × 99 (red) and SPS3 × 1 (blue) are evaluated. Each dot represents a single plant. Equation parameters and model selection criteria are presented in Table 6. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 6

Parameters for the relationship between biomass accumulated at reproductive structures at R5 and plant growth rate (biomass partitioning, Fig. 2a) and seed number per plant as a function of reproductive biomass accumulated at R5 (seed set efficiency, Fig. 2b), for cultivars SPS3 × 1 and SPS4 × 99 evaluated in Exp. 2. The parameter α is the initial slope of the relationship, x_0 is the x value when $y > 0$, and β is the curvature of the relationship (Eq. (1)). The $\Delta AICc$ is the AICc difference between the straight line model and the hyperbolic model (Eq. (1)). Whenever the $\Delta AICc$ is positive, the hyperbolic model has more chances of being the correct model. If negative, the straight line model is the one selected.

Cultivar	(a) Seed number vs Plant growth rate			(b) Reproductive biomass vs Plant growth rate			(c) Seed number vs Reproductive biomass		
	Parameter	Estimate	95% CI	Parameter	Estimate	95% CI	Parameter	Estimate	95% CI
SPS3 × 1	α	141.3	(129.9 to 152.7)	α	10.23	(9.25 to 11.20)	α	13.69	(12.63 to 14.75)
	x_0	0.022	(-0.007 to 0.051)	x_0	-0.050	(-0.801 to -0.001)	x_0	0.096	(-0.192 to 0.383)
	β	0.188	(0.132 to 0.245)	β	0.154	(0.094 to 0.213)	β	0.009	(0.005 to 0.014)
	$\Delta AICc$	63.3		$\Delta AICc$	35.2		$\Delta AICc$	16.26	
	R^2	0.84		R^2	0.80		R^2	0.86	
SPS4 × 99	α	177.3	(161.6 to 193.0)	α	15.69	(14.04 to 17.35)	slope	11.62	(11.37 to 11.88)
	x_0	0.013	(-0.013 to 0.039)	x_0	-0.012	(-0.042 to 0.018)	y-intercept	0.570	(-1.865 to 3.006)
	β	0.168	(0.097 to 0.238)	β	0.265	(0.167 to 0.363)			
	$\Delta AICc$	27.0		$\Delta AICc$	44.27		$\Delta AICc$	-1.21	
	R^2	0.82		R^2	0.77		R^2	0.91	

reduced speeds and at an adequate depth can provide a more uniform plant establishment at minimal cost and are under grower control. Therefore, in this sense, management of planting quality will always be economically relevant due to the low cost-benefit ratio. Second, if the yield response is expressed relative to the non-uniform treatment it ranges from 6.3 to 7.8% for the spatial and temporal effects, respectively. Currently, soybean breeding is improving yield at a rate of 0.5% increase per year (Specht et al., 2014; De Felipe et al., 2016), so yield improvements related to planting quality are equal to 12–15 years of genetic progress.

5. Conclusions

Yield reductions of non-uniform soybean canopies are larger with canopies having temporal rather than spatial planting quality issues. Non-uniform temporal plant-to-plant variability always reduced yield, while non-uniform spatial plant-to-plant variability only reduced yield in the shortest maturity group cultivar and in one out of two experiments.

The relationship between seed number and plant growth during the seed set period was not linear for the two tested cultivars. The effect of temporal non-uniform stands will depend on the increase in individual plant growth rate associated with higher resource availability and on the reduction in seed set and reproductive partitioning associated with higher growth rates. The expected effect of temporal non-uniform canopies ultimately depends on the curvature of the relationship between crop growth rate and seed number. Since this relationship has a strong genetic component, the effect of non-uniform temporal canopies will therefore depend on the specific genotype. Therefore, future research is needed to better understand the interaction between cultivar reproductive characteristics and susceptibility to non-uniform temporal canopies.

There are three main novel findings in our study. First, temporal non-uniform canopies are more associated to soybean yield reductions than spatial non-uniform canopies. Second, yield reductions in non-uniform temporal stands are explained by reduced seed set at dominated plants with higher plant growth rates. Last, the general belief that soybean planting quality problems can be easily solved by increasing plant density is challenged. Our findings describe higher plant densities cannot compensate for non-uniform temporal distributions.

Acknowledgements

Authors want to acknowledge useful comments from JL De Bruin and C Zinselmeier. This research was partially supported by Syngenta Agro Argentina. A Masino was supported by a scholarship from Proyecto Territorial del Este de la Provincia de Córdoba (CORDO-1262101) and Proyecto Nacional Tecnologías de Manejo de Cultivos en Sistemas Basados en Cereales y Oleaginosas (PNCYO 1127032). JL Rotundo and L Borrás are members of CONICET, the Argentina National Research Council.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.eja.2018.02.006>.

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