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Soybean Seed Yield Response to Plant Density by Yield Environment in North America

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ABSTRACT

Inconsistent soybean [*Glycine max* (L.) Merr.] seed yield response to plant density has been previously reported. Moreover, recent economic and productive circumstances have caused interest in within-field variation of the agronomic optimal plant density (AOPD) for soybean. Thus, the objectives of this study were to: (i) determine the AOPD by yield environments (YE) and (ii) study variations in yield components (seed number and weight) related to the changes in seed yield response to plant density for soybean in North America. During 2013 and 2014, a total of 78 yield-to-plant density responses were evaluated in different regions of the United States and Canada. A soybean database evaluating multiple seeding rates ranging from 170,000 to 670,000 seeds ha^{-1} was collected, including final number of plants, seed yield, and its components (seed number and weight). The data was classified in YEs: low (LYE, <4 Mg ha^{-1}), medium (MYE, 4–4.3 Mg ha^{-1}), and high (HYE, >4.3 Mg ha^{-1}). The main outcomes were: (i) AOPD increased by 24% from HYE to LYE, (ii) per-plant yield increased due to a decrease in plant density: HYE > MYE > LYE, and (iii) per-plant yield was mainly driven by seed number across plant densities within a YE, but both yield components influenced per-plant yield across YEs. This study presents the first attempt to investigate the seed yield-to-plant density relationship via the understanding of plant establishment and yield components and by exploring the influence of weather variables defining soybean YEs.

Core Ideas

- Soybean seed yield response to plant density is dependent on yield environment.
- Low yield environments required higher plant densities than high yield environments.
- Plant density mainly affected per-plant seed number.
- No differences in plant survival were observed among yield environments.

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Soybean is the main oilseed crop produced worldwide, occupying 130 million ha with a total production of 360 million Mg (USDA-FAS, 2018). Soybean production costs in the United States increased about 50% over the past decade, with seed cost representing roughly 37% of the total production costs (USDA-ERS, 2018). In addition, seed price increased about 46% due to biotechnology advancements (Shi et al., 2009). Therefore, defining the AOPD for soybean is a critical decision for producers to optimize return on investment. The AOPD is defined as the minimum number of plants (in a per-unit-area basis) required to maximize yield. On the other hand, soybean plant density levels above the AOPD increase the risk of lodging and disease development (Grau et al., 1994; Peltier et al., 2012) without adding a yield benefit, reinforcing the need for defining the AOPD for this crop.

Different environmental, genotypic, and crop management conditions (maturity group, sowing date, genotype, climate, and soil) affect soybean yield (Ball et al., 2000; Gan et al., 2002; Agudamu and Shiraiwa, 2016) and therefore can help to explain variations in yield response to plant density (Wells, 1993; Ball et al., 2000; Norsworthy and Frederick, 2002). For example, adverse environmental conditions limit soybean plasticity, requiring an increase in plant density to offset the reduction in the branching ability (Carpenter and Board, 1997). Soybean seed yield response to plant density has not shown consistent results, with a lack of response in some cases (Board, 2000; Cox et al., 2010), and showing clear responses in other studies (Egli, 1988; Gan et al., 2002; Holshouser and Whittaker, 2002; Lee et al., 2008; Walker et al., 2010; de Luca and Hungria, 2014). However, the AOPD in these studies broadly ranged from 70,000 to 600,000 plants ha^{-1} (Egli, 1988; Holshouser and Whittaker, 2002).

Recent studies in maize (*Zea mays* L.) (Assefa et al., 2016, 2018a), canola (*Brassica napus* L. 'Canola') (Assefa et al., 2018b), and soybean (Corassa et al., 2018) proposed classifying each

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Abbreviations: AOPD, agronomic optimal plant density; HYE, high yield environment; LYE, low yield environment, MYE, medium yield environment; YE, yield environment.

study in a YE based on its average productivity. Thus, for soybean in Brazil, Corassa et al. (2018) indicated that seeding rate could be reduced by 18% when moving from low (<4 Mg ha^{-1}) to high (>5 Mg ha^{-1}) YE. Similar results might be expected for soybean grown in North America, but this assumption should be tested. Therefore, a broad database comprised of studies evaluating soybean seed yield response to plant density in varying YEs could assist in providing an unbiased analysis focused at both local and regional levels.

Several soybean studies evaluated changes in yield components due to variations in plant density. These studies indicated that a decrease in plant density produces greater growth of individual plants (Epler and Staggenborg, 2008; Cox et al., 2010; de Luca and Hungria, 2014) and consequently more leaf area, branches, pods, and seeds per plant (Egli, 1988; Lee et al., 2008; Cox et al., 2010). However, in low productive environments, variations in per-plant leaf area and yield components at low plant density might not compensate for the lack of plants required to maximize light interception, for improving canopy photosynthesis, growth rate, and, ultimately, yield (Board and Harville, 1994; Ball et al., 2000; Gaspar and Conley, 2015; Lee et al., 2008).

The objectives of the current study were to: (i) determine the AOPD for varying YEs and (ii) study variations in yield components (seed number and weight) related to the changes in seed yield response to plant density for soybean.

MATERIALS AND METHODS

Data Description

The data evaluated in the current analysis were obtained from trials performed during 9 site-years where four different seeding rates were evaluated in combination with six different relative maturities and, in some situations, two row spacings (Table 1). As the main objective of this project was to evaluate the effect of plant density (obtained from different seeding rates) on seed yield response, each combination of relative maturity and row spacing within each site-year was considered as an independent study. In detail, 78 soybean yield-to-plant density responses (1344 data points, Fig. 1A) across relative maturities, row spacings and locations (herein termed studies) were evaluated in different regions of the United States (Illinois, Indiana, and Iowa) and Canada (Ontario) by DuPont Pioneer (Johnston, IA) researchers during the 2013 and 2014 growing seasons. Thus, a wide range of climatic conditions was explored (annual average temperature was 10.5, 10.7, 8.8, and 8.3°C; and total annual rainfall 1008, 990, 876, and 785 mm for Illinois, Indiana, Iowa, and Ontario, respectively). The experimental design used was a randomized complete block design (RCBD) with four to six replications (plot size 4.6 by 3 m). Seeding rates ranged from 170,000 to 670,000 seeds ha^{-1}, reaching final plant densities from 60,000 to 650,000 plants ha^{-1}. All field studies were planted with 38 and/or 76 cm row spacing, managed with conventional till (chisel plowed or disked), in rainfed environments, and using relative maturities ranging from 2.5 to 4.2. A total of 16 indeterminant soybean varieties were included in the studies among important commercially available DuPont Pioneer Brand soybean products. Additionally, plots were uniformly fertilized with all recommended nutrients for their respective region. As necessary, weeds, diseases, and insects were controlled according to the rec-

Table 1. Soybean database information: year, site, latitude, longitude, soil type, total rainfall and average daily mean temperature during soybean growing season, planting date, seeding rate, row spacing, relative maturity evaluated, and mean (standard deviation, SD) values for the variables evaluated (plant density, seed yield, seed number, and 1000-seed weight).

Year	Site	Latitude	Longitude	Soil type (USDA)	Rainfall	Daily mean temperature	Planting date	Seeding rate	Row spacing	Relative maturity	Plant density	Seed yield	Seed no.	1000-seed weight
					mm	°C		×1000 seeds ha^{-1}	cm		×1000 plants ha^{-1}	Mg ha^{-1}	seed m^{-2}	g
2013	Illinois-1	40.06° N	88.41° W	Aquic Argiudoll	428	19.1	19 May	185;310;430;555	38	(3.5;3.6;3.7;3.8;3.9;4.2)	312 (128)	3.82 (0.48)	2256 (314)	170 (14.1)
							19 May	185;310;430;555	76	(3.5;3.6;3.7;3.8;3.9;4.2)	290 (107)	3.87 (0.50)	2245 (345)	174 (13.4)
	Illinois-2	39.92° N	88.21° W	Aquic Argiudoll	393	19.7	20 May	170;270;370;470	76	(3.5;3.6;3.7;3.8;3.9;4.2)	271 (94)	3.20 (0.40)	1914 (245)	168 (12.7)
	Indiana	40.28° N	86.06° W	Typic Endoaquoll	491	17.8	8 May	170;270;370;470	76	(2.8;3.0;3.1;3.2;3.4;3.5)	237 (65)	4.51 (0.37)	2482 (270)	183 (17.5)
	Ontario	42.37° N	82.19° W	Mollic Endoaquept	496	17.0	14 May	185;310;430;555	76	(2.5;2.6;2.7;2.8;2.9;3.2)	329 (122)	3.88 (0.69)	2186 (353)	177 (11.2)
2014	Illinois-1	40.06° N	88.42° W	Aquic Argiudoll	757	18.2	23 Apr	370;470;570;670	38	(3.5;3.6;3.7;3.8;3.9;4.2)	273 (82)	4.36 (0.34)	2303 (244)	190 (15.1)
							23 Apr	170;270;370;470	76	(3.5;3.6;3.7;3.8;3.9;4.2)	184 (74)	4.16 (0.58)	2259 (355)	185 (14.3)
	Illinois-2	39.92° N	88.22° W	Aquic Argiudoll	601	18.0	24 Apr	370;470;570;670	38	(3.5;3.6;3.7;3.8;3.9;4.2)	434 (94)	4.50 (0.35)	2327 (303)	195 (16.3)
							24 Apr	170;270;370;470	76	(3.5;3.6;3.7;3.8;3.9;4.2)	254 (83)	4.48 (0.39)	2373 (289)	190 (15.6)
	Indiana	40.36° N	85.99° W	Typic Endoaquoll	622	16.6	23 May	185;310;430;555	76	(2.8;3.0;3.1;3.2;3.4;3.5)	153 (53)	4.43 (0.51)	2389 (306)	184 (21.4)
	Iowa	42.21° N	92.37° W	Typic Endoaquoll	600	16.2	21 May	370;470;570;670	38	(2.5;2.6;2.7;2.8;2.9;3.2)	425 (68)	3.98 (0.34)	2217 (253)	181 (13.8)
							21 May	170;270;370;470	76	(2.5;2.6;2.7;2.8;2.9;3.2)	281 (61)	4.11 (0.37)	2246 (251)	184 (13.8)
	Ontario	42.37° N	82.23° W	Mollic Endoaquept	525	16.4	24 May	185;310;430;555	76	(2.5;2.6;2.7;2.8;2.9;3.2)	324 (113)	4.26 (0.36)	2318 (141)	184 (13.2)

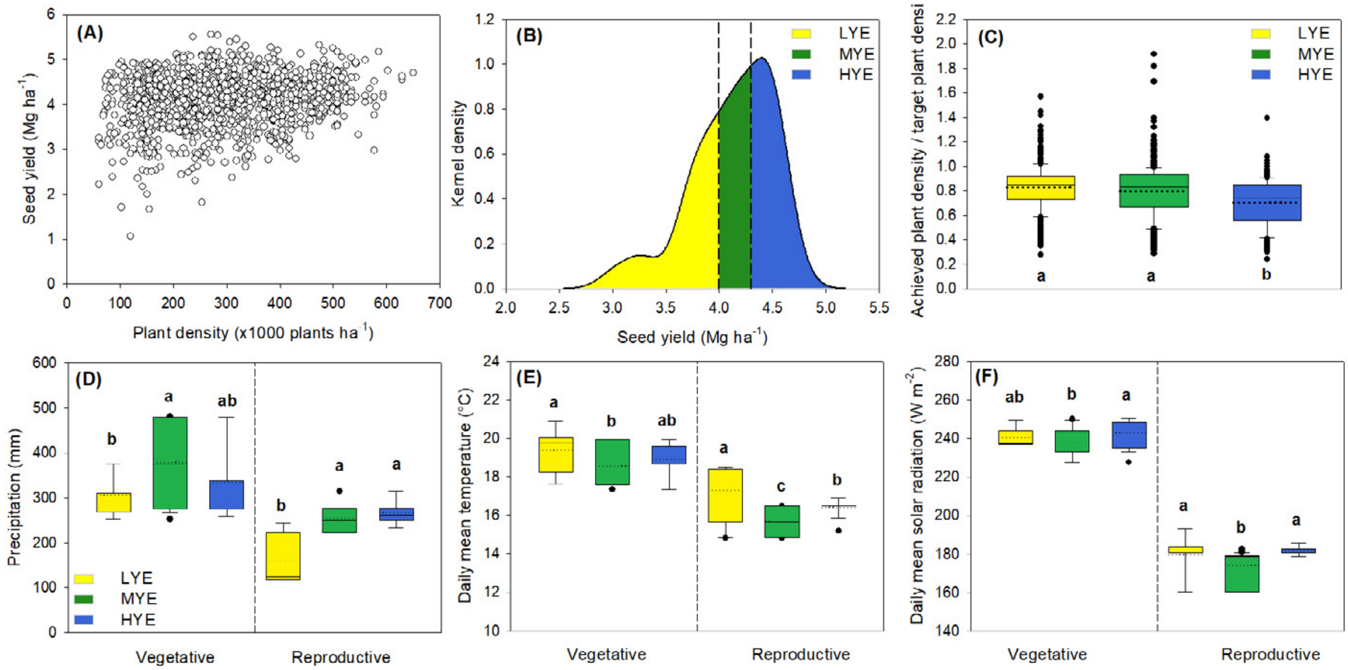

Fig. 1. Relationship between (A) seed yield and plant density, (B) density distribution of average seed yield for each study and yield environments classified by terciles (low yield environment, LYE, <4.0 Mg ha^{-1}; medium yield environment, MYE, 4.0 to 4.3 Mg ha^{-1}; and (C) high yield environment, HYE, >4.3 Mg ha^{-1}), box plots portraying the ratio between the achieved plant density and the target plant density; (D) average accumulated precipitation, (E) daily mean temperature; and (F) daily mean solar radiation for vegetative (May–July) and reproductive (August–October) periods for LYE, MYE, and HYE. The box plots portray the fifth (lower whisker), 25th (bottom edge of the box), 75th (top edge of the box), and 95th (upper whisker) percentiles. The solid line within the box represents the median, the dotted line the mean, and the circles referred to outliers. Different letters in the same growing period and panel indicate differences between YEs using Bayes inference.

ommended management practices for each site. Additional information on the database is described in Table 1.

After physiological maturity (R_8, Fehr and Caviness, 1977) seed yield was determined for each plot by harvesting the central rows (two rows for 76 cm and four rows for 38 cm), measuring seed moisture, and adjusting yields to 130 g kg^{-1} moisture content. A 300-seed sample was dried at 60°C until constant weight and weighed to calculate the 1000-seed weight adjusted to 130 g kg^{-1} moisture content. Seed yield and 1000-seed weight data were used to quantify the per-unit-area seed number. Also at R_8 stage, the final plant density was determined and later used to calculate the ratio between achieved and target plant density (Fig. 1C). Plant density was also used to calculate the per-plant seed yield and seed number using the per-unit-area yield and seed number, respectively.

Soybean seed yield was evaluated with two approaches, expressed as:

$$\text{Seed yield} = \text{seed number (seeds ha}^{-1}) \times \text{seed weight (mg seed}^{-1}) \quad [1]$$

$$\text{Seed yield} = \text{plant density (plants ha}^{-1}) \times \text{per–plant yield (g plant}^{-1}) \quad [2]$$

Where per-plant yield could be expressed as:

$$\text{Per–plant yield} = \text{per–plant seed number (seeds plant}^{-1}) \times \text{seed weight (mg seed}^{-1}) \quad [3].$$

Weather data (precipitation, daily mean temperature, and solar radiation) were obtained for each site-year from Climate Engine (Huntington et al., 2017) for the United States and from Government of Canada web page (http://climate.weather.gc.ca) for Canada data. Weather data from each site-year was divided into approximate vegetative (involving from May–July) and reproductive (from August–October) periods, although detailed phenology within the soybean growing season was lacking. This analysis permitted a characterization of potential scenarios for early- vs. late-season weather conditions for soybeans in each site-year in relation to the yield classification developed (YEs) (Fig. 1B, 1D–1F).

Statistical Analysis

The average yield for each plant-density response evaluated (78 total studies, Table 1) was used to classify the dataset in different YEs (Corassa et al., 2018). This method acknowledges that variations within a study are only due to the treatment (plant density). The kernel density distribution of yield data (average yield for each study) was divided into terciles (<33%, 33–66%, and >66%) (Fig. 1B), obtaining a balanced number of studies across YEs (26 studies in each YE). Thus, low (LYE, <4 Mg ha^{-1}), medium (MYE, 4.0–4.3 Mg ha^{-1}), and high (HYE, >4.3 Mg ha^{-1}) YEs were defined.

To identify soybean seed yield variation accounted for known factors after removing the plant density effect, a hierarchical mixed model was fitted. Yield environment (site-year combinations), row spacing, relative maturity, planting date (Julian days), and their respective interactions, were considered as random effects, whereas plant density was considered as fixed effect.

The variance was estimated using the nlme (Pinheiro et al., 2018) in R program (R Core Team, 2018).

Linear regression with plateau was implemented to quantify the soybean yield response to plant density. Instead of fitting regression models using standard approaches, such as the Ordinary Least Square (OLS) method, which results in a single fit that minimizes the sum of squared errors from the data, we used hierarchical Bayesian models allowing us to explore all the possible regression lines (combinations of intercepts, slopes, and breakpoints) in all the hierarchical levels considered in this study. Thus, calculating the most probable AOPD at each YE. Two hierarchical levels were considered in this analysis: field-level (studies) and YE-level (LYE, MYE, and HYE–each YE in this level is a set of different studies). Each coefficient (intercept, slope, and breakpoint) were assumed to follow a normal distribution $\sim N(m_i, l_i^{-1})$, where *i* represented the different coefficients. Thus, we set six probability distributions (i.e., priors) in our model, three normal priors for the averages and three γ priors for the precisions. The precision parameter is defined as the reciprocal of the variance: the higher the precision, the lower the variation. All prior distributions were set to assume large variances, having little influence on the analysis relative to the observed data (Kyveryga et al., 2013). The model was run independently for each YE using the same set of priors to avoid any subjectivity. Subsequent distributions were obtained using Markov-chain Monte Carlo simulation (Gelman and Hill, 2007) with a Gibbs sampling algorithm with 15,000 random draws after a warm up period of 5000 interactions. The *rjags* package (Plummer et al., 2018) was used to build the models. Further details of the model used in this study can be found in Corassa et al. (2018).

Linear relationships between soybean seed yield and yield components (seed number and 1000-seed weight) were fitted using the lm procedure included in R software (R Core Team, 2018). To study the relationship between per-plant seed yield, yield components, and plant density, the dataset was divided into quartiles (Q) depending on the plant density. Thus, plant densities dividing the different Q were: <190,000; 190,000–290,000; 290,000–379,000; and >379,000 plants ha^{-1}. For these variables, comparisons between Q within a YE and between YEs within a Q were done using Bayes inference implemented in R with the BEST package (Kruschke and Meredith, 2018). In addition, the relationship between the achieved- and the target-plant density (seeding rate) was compared among YEs using Bayes inference. This approach has several advantages compared to the traditional *t* test, such as the opportunity to incorporate non-normal data distributions, unequal variances, and unbalanced sample size (Kruschke, 2013). Lastly, weather data (precipitation, daily mean temperatures, and solar radiation) were compared among YEs for vegetative and reproductive periods using Bayes inference. Thus, weather data for each YE was weighed and determined by the number of studies within site-years comprising a YE.

RESULTS

Seed Yield and Plant Density

Seed yield variability across all 78 studies was mainly explained by YE (39.9% of the variance), followed by planting date within YE (6.1% of the variance) (Table 2). The relative maturity and row spacing (both within YE) accounted for 2.3 and 1.7% of the variance, respectively. Lastly, most of the seed yield variability (47.2%) was due to unexplained factors (residual). Thus, other factors that differed beyond those evaluated in the current study should be considered to explain the variability in soybean seed yield.

For the pooled data, a seed yield response to plant density was not observed (Fig. 1A), although some data points represented plant density lower than 300,000 plants ha^{-1} and seed yield below 3 Mg ha^{-1}, substantially lower than the overall seed yield average for the entire dataset, 4.1 Mg ha^{-1}. However, when the studies were classified by YE, significant yield responses to plant density occurred in the different YEs (Fig. 2). For the LYE the most probable AOPD was 313,000 plants ha^{-1} (Fig. 2A), decreasing to 236 and 240,000 plants ha^{-1} in the MYE (Fig. 2B) and HYE (Fig. 2C), respectively. This is a 24% decrease in AOPD from LYE to MYE and HYE.

Low plant densities in the LYE highly penalized seed yield. For example, at a plant density of 200,000 plants ha^{-1} in the LYE seed yield decreased by 12% compared with the maximum yield (plateau) obtained for this YE (4.3 Mg ha^{-1}). Meanwhile, at the same above mentioned plant density level, seed yield only decreased by 5% for the MYE and by 4% for the HYE relative to their respective plateau yield levels for these YEs (plateau at 4.5 and 4.7 Mg ha^{-1}, respectively).

The cumulative probability of the AOPD at each YE (Fig. 3A) showed a greater difference for the LYE compared with both MYE and HYE. For example, the maximum probability for reaching the AOPD with less than 250,000 plants ha^{-1} was 58% for both the MYE and HYE but was reduced to 17% for the LYE. In addition, there is a 90% of probability of the AOPD being lower than 400,000; 321,000; and 340,000 plants ha^{-1} for the LYE, MYE, and HYE, respectively (Fig. 3A). Additionally, the probability analysis showed that the 50% interquartile range (between 25 and 75 quartiles) for the AOPD ranged between 268,000 and 355,000 plants ha^{-1} for the LYE, 191,000 and 282,000 plants ha^{-1} for the MYE, and 187,000 and 290,000 plants ha^{-1} for the HYE (Fig. 3B).

Yield Components

Soybean seed yield according to Eq. [1], is the product of seed number and weight components. Following this rationale, per-unit-area seed number (seeds ha^{-1}) accounted for a variation of 75, 39, and 44% in seed yield for the LYE, MYE, and HYE, respectively (Fig. 4A). On the other hand, 1000-seed weight slightly accounted for small changes in yield (11%) for the LYE and MYE, whereas a relationship was not observed in the HYE (Fig. 4B).

Another way to analyze seed yield components is to consider the relationship between per-unit-area number of plants and the per-plant yield. Thus, based on Eq. [2] and [3], seed yield components were further investigated (Fig. 5). Per-plant seed yield increased as plant density decreased in all YEs (Fig. 5A–5D). A greater increase in per-plant yield with decreasing plant density was observed for the HYE compared to MYE and LYE. Thus, when moving from Q_4 (avg. 454,000 plants ha^{-1}) to Q_1 (avg. 146,000 plants ha^{-1}), per-plant yield increased an average of 306% for the HYE, 260% for the MYE and 253% for the LYE. The same trend was followed by the per-plant seed number (Fig. 5 E–5H), accounting for a major proportion of the per-plant yield variation. Thus, both variables showed strong linear

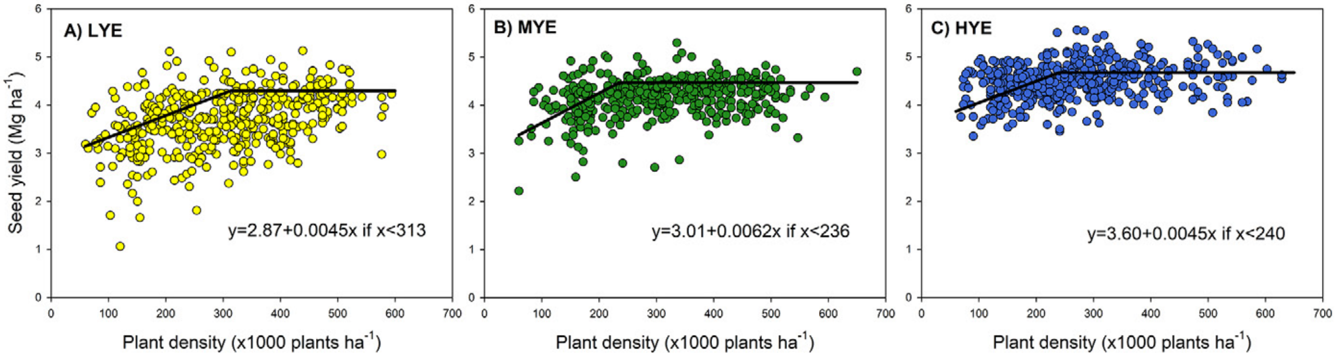

Fig. 2. Relationship between seed yield (Mg ha^{-1}) and plant density (plants ha^{-1}) for (A) low (LYE, <4.0 Mg ha^{-1}), (B) medium (MYE, 4.0–4.3 Mg ha^{-1}), and (C) high yield environments (HYE, >4.3 Mg ha^{-1}). Models were fitted using hierarchical Bayesian models.

relationships for all YEs (R^2 > 0.96, data not shown). On the other hand, in the LYE and MYE, changes in the 1000-seed weight were not observed with variations in plant density, averaging 175 g in the LYE and 184 g in the MYE (Fig. 5I–5L). In contrast, 1000-seed weight increased by 4% (from 184 to 191 g) from lower (Q_1) to higher plant density levels (Q_4) in the HYE.

It is worth noting the high degree of variation, represented by a wider size of the whiskers (Fig. 5A, 5E), in both per-plant yield and seed number across all YEs at Q_1 relative to the rest of the quartiles. For plant densities above 190,000 plants ha^{-1} (>Q_1) the variability observed for these two variables was substantially reduced. Thus, a high degree of uncertainty or risk associated with planting to achieve low densities was documented for per-plant yield and seed number regardless of the YE. Conversely, planting higher densities reduced the variability for all yield components with exception of the seed weight.

Per-plant yield varied between YEs at all plant densities (Fig. 5A–5D). However, the magnitude of the difference in per-plant yield between YEs was greater at low (<190,000 plants ha^{-1}, Q_1) rather than high plant densities (>379,000 plants ha^{-1}, Q_4). For Q_1, per-plant yield for MYE and HYE was 9 and 35% greater than per-plant yield for the LYE, respectively; and these differences were reduced to 7 and 12% for Q_4.

Per-plant yield differences between YEs were explained by both per-plant seed number and weight (Fig. 5E–5L), except at high plant densities (Q_4) where only 1000-seed weight varied among YEs. Thus, for Q_1, the average per-plant seed number was 140, 146, and 182 seeds plant^{-1} in the LYE, MYE, and HYE, respectively (Fig. 5E). In contrast, differences in per-plant seed number were not observed between YEs for Q_4 (avg. 51, 52, and 52 seeds plant^{-1} for LYE, MYE, and HYE, respectively; Fig. 5H). On the other hand, 1000-seed weight in the LYE for Q_1 was smaller than 1000-seed weight in the MYE and HYE (avg. 176, 184, and 184 g for LYE, MYE, and HYE, respectively; Fig. 5I). However, for the Q_4 average 1000-seed weight followed the order: LYE (175 g) < MYE (185 g) < HYE (191 g) (Fig. 5L).

Table 2. Estimation of soybean seed yield variance components considering environmental (yield environment [YE]) and management factors (planting date, row spacing, and relative maturity).

Source of variation	Variance
	%
YE†	39.9
YE: planting date (PD)	6.1
YE: relative maturity (RM)	2.3
YE: row spacing (RS)	1.7
YE: RM: PD: RS	2.8
Residual	47.2
Total	100

† Studies are nested into the YE.

In summary, at low plant densities both per-plant seed number and 1000-seed weight explained differences in per-plant yield among YEs, whereas at high plant densities, differences among YEs in per-plant yield were mainly explained by 1000-seed weight.

DISCUSSION

Seed Yield and Plant Density

Soybean seed yield variability was mainly explained by the YE, followed by planting date, variety relative maturity, and row spacing factors (Table 2). This is supported by the reported reductions in seed yield due to the delay on planting dates (Kratochvil et al., 2004; Lee et al., 2008), the use of short relative maturities (Edwards and Purcell, 2005; Lee et al., 2008), and the use of wide row spacings (Andrade et al., 2019; Holshouser and Whittaker, 2002; De Bruin and Pedersen, 2008).

Seed yield response to plant density depended on the YE (Fig. 2). Similar results were reported by Wells (1991), indicating that seed yield responded to plant density with less favorable environments but lack of yield to plant density response was documented when environmental conditions were more favorable for improving overall productivity. Likewise, for canola, with similar vegetative and reproductive plasticity as soybean (Rondanini et al., 2017), Assefa et al. (2018b) reported negligible yield responses to plant density in MYE and HYE but greater yield responses in LYE.

According to the current study, plant density could be reduced from 313,000 to 238,000 plants ha^{-1} from the LYE to the MYE and HYE, without negatively impacting soybean seed yield. It should be consider that this result was obtained with indeterminant varieties and based on previous studies (Gan et al., 2002; Agudamu and Shiraiwa, 2016) is possible to get a greater effect of plant density on seed yield with determinant varieties. However, further research is needed for exploring the yield to plant density relationship for determinant soybean varieties. Similar to the results observed in the current study, but for seeding rate, which mainly determines the plant density, were recently reported in Brazil by Corassa et al. (2018). These authors reported that the most probable optimal seeding rate could be reduced by 18% from LYE compared to HYE (from 290,000 to 245,000 seeds ha^{-1}, respectively). Previous studies

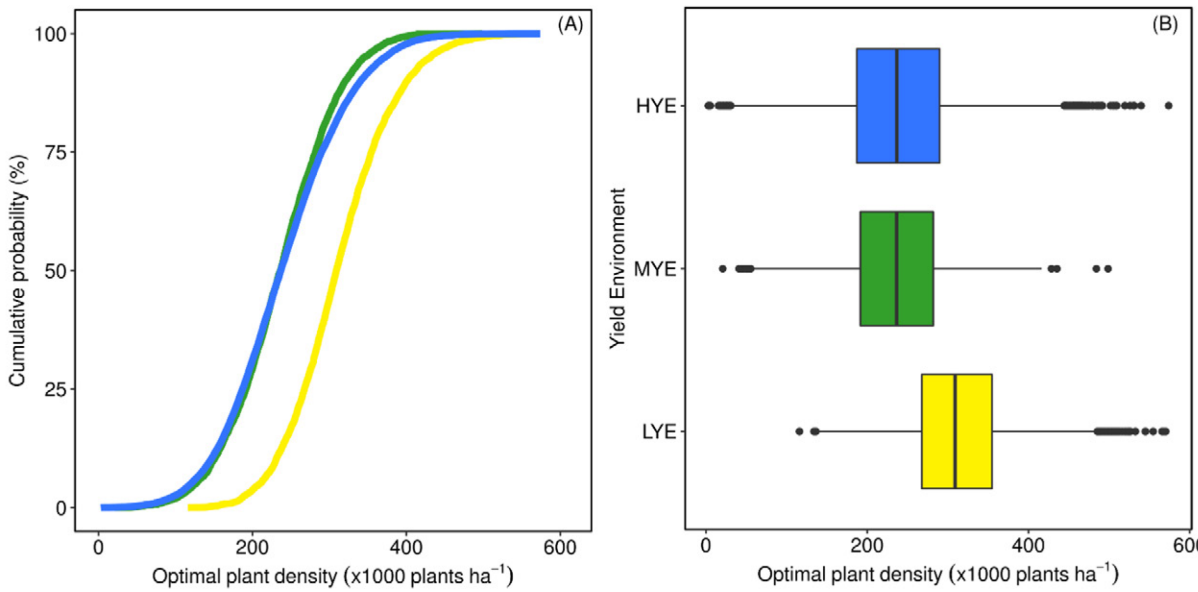

Fig. 3. Cumulative probabilities (%) of (A) agronomic optimal plant density (AOPD, plants ha^{-1}); and (B) AOPD range to achieve the plateau-level for the seed yield-to-plant density relationship for the low (LYE, in yellow), medium (MYE, in green), and high yield environment (HYE, in blue). For panel B, box plots portray the 25th (bottom edge of the box) and the 75th (top edge of the box). The solid line within the box represents the median and the circles referred to outliers.

conducted under varied environments in the United States (Ball et al., 2000; Heatherly and Elmore, 2004; Lee et al., 2008, De Bruin and Pedersen, 2009, Epler and Staggenborg, 2008; Walker et al., 2010; Gaspar and Conley, 2015), Brazil (de Luca et al., 2014), and Japan (Agudamu and Shiraiwa, 2016; Matsuo et al., 2018) also reported different values of AOPDs that were within the range of AOPDs observed in the current study, ranging from 238,000 to 313,000 plants ha^{-1}.

A recent study hypothesized that low plant establishment and survival in a LYE could be one of the potential factors affecting the differential yield response to seeding rate between YEs (Corassa et al., 2018). However, in the current study, results similar to those reported by these authors were obtained by evaluating plant density as an independent variable instead of seeding rate (Fig. 2). Moreover, the current work portrayed greater plant establishment (relative to the target seeding rate) for the LYE, with the plant density-to-target seeding rate ratio following the order from high to low: LYE > MYE > HYE (Fig. 1C). Therefore, this study refutes the hypothesis that a greater AOPD in a LYE is related to a lower plant survival rate relative to the HYE.

A second hypothesis from Corassa et al. (2018) is related to differential capacity to intercept solar radiation for HYE relative to LYE which affects reproductive ability of soybean plants for setting more pods and seeds on a per-plant scale. Previous studies indicated that AOPD increased when utilizing shorter soybean maturity group varieties and with later planting dates (Holshouser and Whittaker, 2002; Kratochvil et al., 2004; Lee et al., 2008). Those situations promoted shorter vegetative periods, resulting in small plants with poor light interception and reduced canopy photosynthesis (Ball et al., 2000; Gaspar and Conley, 2015), impacting reproductive plant growth rate and, consequently, decreasing yields (Wells, 1991; Ball et al., 2000; Lee et al., 2008). In addition, late planting dates will experience seed-filling periods with below optimal temperature and solar radiation, lowering the overall plant growth rate because of the lower conversion efficiency of soybean (Andrade, 1995). Moreover, delayed plantings shortened the soybean seed-filling period (Major et al., 1975). These processes could partially explain the differences in AOPD observed in the current study (Fig. 2). As for other potential factors contributing to explain AOPD variations, the average relative maturity was 3.2 for both LYE and MYE and 3.5 for HYE, while the average planting date was 12 d before in the HYE with respect to the LYE and MYE.

Seasonal water supply also affects soybean AOPD, with an overall increase in plant density required to maintain seed yield under drought relative to well-watered condition (Ball et al., 2000; Holshouser and Whittaker, 2002). However, the strategy of increasing plant density would not be adequate under progressive and more severe drought conditions in which water consumption by soybean should be delayed and be saved until later and more critical reproductive stages (pod formation and seed-filling periods). In this scenario, water use must be regulated by reducing plant density and considering other management practices such as increasing row width and/or reducing the maturity group (Frederick et al., 2001; Wei et al., 2018).

A simple analysis of the average weather conditions for the three YEs (Fig. 1D–1F) showed that the cumulative precipitation during the late-season soybean growth period (reproductive) was 39% lower in LYE compared with MYE and HYE (Fig. 1D). Related to this, previous studies reported that drought stresses during early reproductive growth stages reduced per-plant leaf area (Wei et al., 2018) and number and length of branches (Frederick et al., 2001; Demirtas et al., 2002), and consequently seed yield was also reduced. Moreover, average daily mean temperature for the reproductive period was 8% higher in LYE compared to MYE and HYE (Fig. 1E) which could exacerbate the effect generated by the lower precipitation in the LYE. This study presents a unique approach to characterize soybean seed yield response to plant density within different YEs and related YEs weather conditions during the soybean growth cycle. But we recognize that further investigation is required on this topic and on exploring other factors defining YEs and the targeted AOPD for soybean.

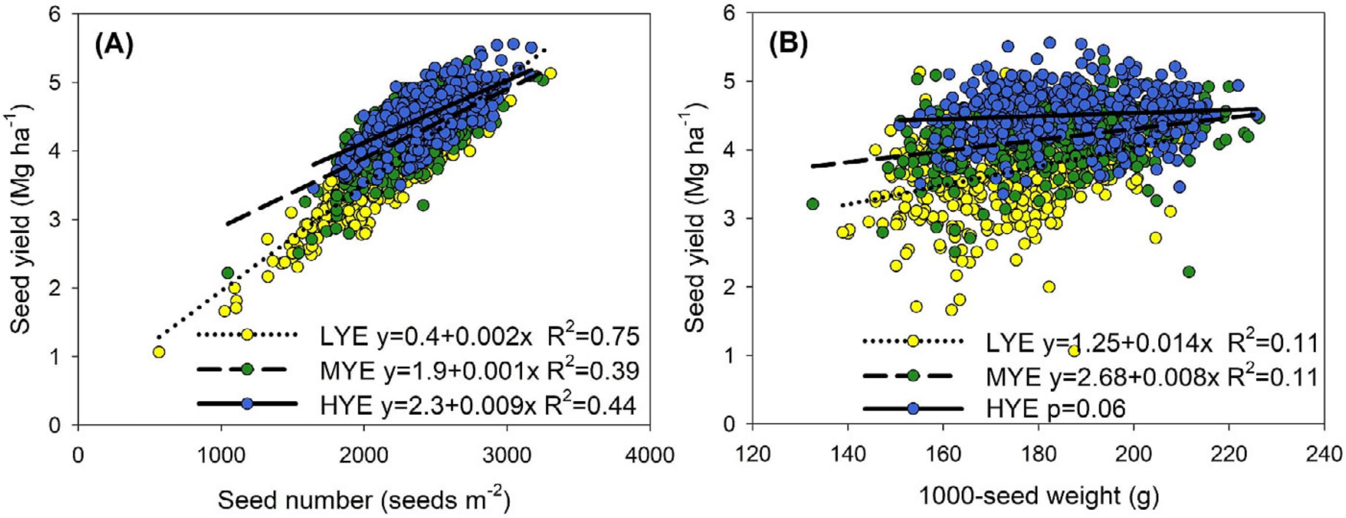

Fig. 4. Relationship between seed yield (Mg ha^{-1}) vs. (A) seed number and (B) thousand-seed weight for the low (LYE), medium (MYE), and high (HYE) yield environments.

In summary, environmental conditions (e.g., water availability, temperature, and radiation), as well as other factors such as fertility or pests, could affect soybean leaf enlargement and branching, reducing crop growth rate and consequently negatively affecting soybean reproductive ability (Boyer, 1970; Ball et al., 2000). Therefore, variation in environmental conditions producing different yield potential (and YEs) affects the final AOPD for soybean. A remarkable point related to this is the way to reach the plant density required. The final plant density is going to be mainly defined by the seeding rate, but other factors could affect the plant establishment and survival. Thus, seed quality (viability and germination rate) and emergence mortality (determined by soil temperature, moisture, weather conditions as well as pest and management practices) are going to affect the relationship between the achieved and the target plant density.

For maize, differential grain yield responses to plant density were also reported according to the YE (Assefa et al., 2016, 2018a; Schwalbert et al., 2018). However, differences in reproductive abilities between maize and soybean generate opposite yield and plant density relationships between crops. With low plant densities, small increases in per-plant grain number are common in response to high plant growth rates for maize; while no limitations in per-plant seed number occurred at high plant growth rates (low plant densities) in soybean (Vega et al., 2001a, b). On the other hand, the contrasting behavior observed at high plant densities is explained by a higher plant growth rate threshold, below which no seed is set for maize relative to soybean (Vega et al., 2001a,b). Thus, maize usually shows a low capacity to produce additional reproductive structures per plant in response to low densities, diminishing the ability of the plant to increase per-plant yield; while ear development is commonly suppressed at high plant densities, especially with older hybrids (Andrade, 1995; Vega et al., 2001a, b; Sarlangue et al., 2007; Di Matteo et al., 2016). In contrast, results from the current study documented the ability of soybean to express lower variation in seed yield at changing plant densities, especially for the MYE and HYE. For LYE, an increase in plant density is a sound strategy directed to compensate for low branching and low leaf expansion and to improve radiation interception by the crop during the critical stages for seed yield determination. In soybean, radiation interception is improved with no penalties in assimilate partitioning to reproductive structures during those periods because of the low threshold values of plant growth rate to set seeds (Vega et al., 2001a, b).

Results of this study showed that AOPD depends on the YE. This is valuable information for site-specific management strategies, such as variable seeding rate. Thus, this information could be considered in fields with different YEs, where seeding rates, and therefore plant density, could be adjusted for each YE, with both economic and agronomic benefits for growers. In this way, adjusting plant density reduces risks of yield losses due to suboptimal densities in a LYE, while limiting higher seed costs due to supra-optimal densities, especially for MYE and HYE. Additionally, it should be considered that supra-optimal densities contribute to both increased lodging risks and potentially increasing the incidence of diseases such as Sclerotinia stem rot (*Sclerotinia sclerotiorum*) due to dense and closed canopies (Peltier et al., 2012; Jaccoud-Filho et al., 2016).

Yield Components

Per-unit-area seed number primarily explained the variations in seed yield (Fig. 4A). Board et al. (1999) indicated that the strength of correlations between seed number and yield was almost twice as large compared with the effect of seed weight for soybean. Both Gaspar and Conley (2015) and Wells (1991) found a high degree of correlation between seed yield and seed number (r = 0.98), whereas seed weight was not correlated to yield. Similarly, Ball et al. (2000) and Gan et al. (2002) reported that the reductions in seed yield caused by low plant densities were due to low seed number on a per-unit-area basis.

As indicated by Carpenter and Board (1997), seed yield response to plant density is defined by a balance between the reduction in per-plant yield and the increase in per-unit-area yield due to the effect of adding plants. In LYE scenarios, per-plant yield adjustments did not offset the reduction in the number of plants as plant density was reduced. Similar results were obtained by Ball et al. (2000) and Gan et al. (2002), reporting an overall increase in per-unit-area yield as plant density increased with a reduction in per-plant yield. On the other hand, for this study, seed weight did not change with

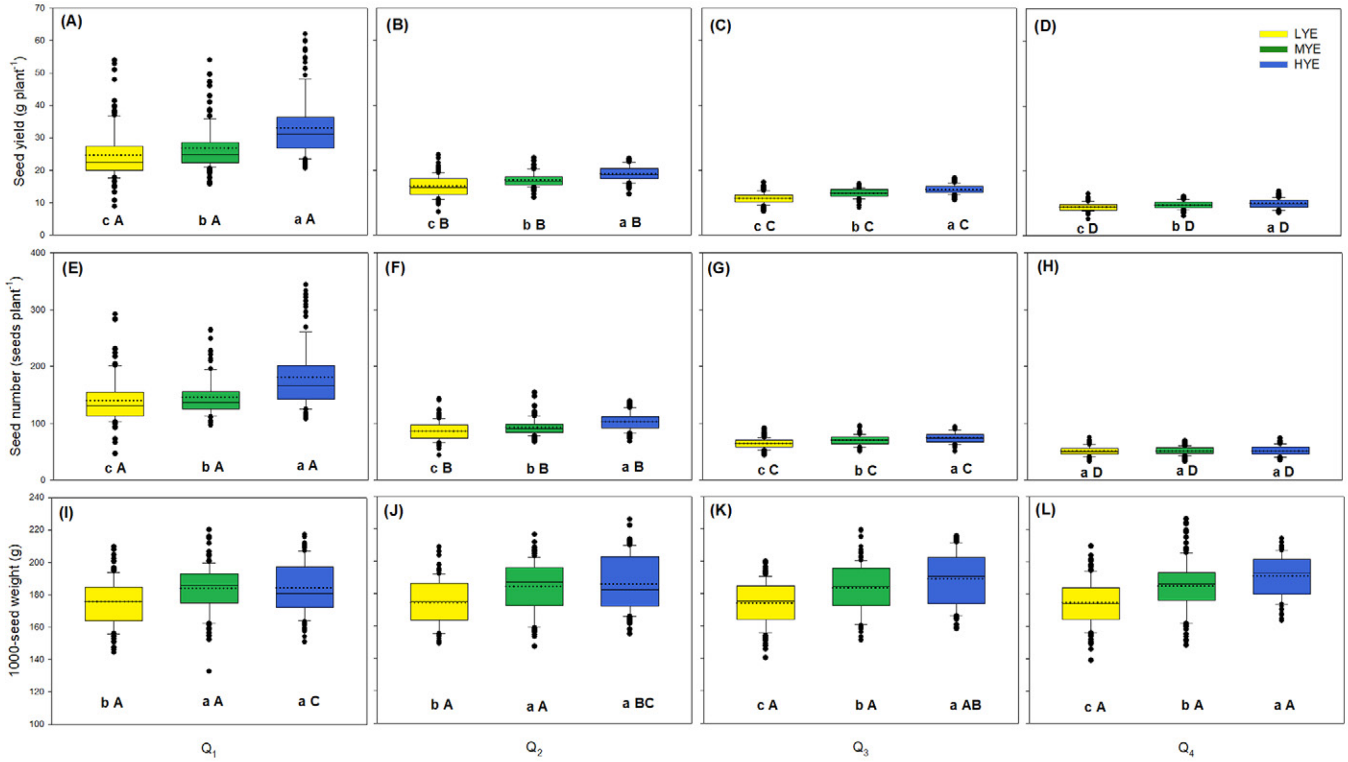

Fig. 5. Box plots portraying the per-plant seed yield (A–D), seed number (E–H), and 1000-seed weight (I–L) for the first (Q_1, A, E, and I), second (Q_2; B, F, and J), 3th (Q_3, C, G, and K), and fourth (Q_4, D, H, and L) quartiles of the plant density distribution data for low (LYE), medium (MYE), and high (HYE) yield environments. Average plant density for each Q was 146,000; 243,000; 330,000; and 454,000 plants ha^{-1} for Q_1, Q_2, Q_3, and Q_4, respectively. The box plots portray the fifth (lower whisker), 25th (bottom edge of the box), 75th (top edge of the box), and 95th (upper whisker) percentiles. The solid line within the box represents the median, the dotted line shows the mean, and the circles are outliers. Different lower-case letters in the same panel indicate differences between YEs and different capital letters within each variable and YE indicate differences between quartiles using Bayes inference.

plant density in the LYE and MYE, but this factor increased at high plant densities (Q_4) in the HYE (Fig. 5I–5L). In agreement with the results observed in LYE and MYE, Board et al. (1999), Norsworthy and Frederick (2002), and Cox et al. (2010) indicated that seed weight did not respond to plant density. However, Elmore (1991) and De Bruin and Pedersen (2008) reported 4 to 5% increases in seed weight as plant density increased, in accordance with the results reported for the HYE. Egli et al. (1987) observed that seeds from flowers developed early in the flowering period were generally larger than those coming from flowers developed later. Considering this, Egli (1988) suggested that the reduction in per-plant seed number with high plant densities was related with a greater proportion of seeds coming from early flowers, allowing an increase in seed weight. This could explain the results observed in the HYE where the favorable growing conditions promoted a high activity of the source throughout the reproductive period and consequently allowed an increase in seed weight. However, restricted growing conditions in the LYE and MYE probably limit the plant's ability to support seed demand (more source-limited), without improving the overall seed weight as plant density increased. Generally, the restricted plant growth and production conditions characterizing LYE and, to a lesser extent MYE, explained the differences in seed weight among YEs.

Overall, the main findings summarized in this current study and in Corassa et al. (2018) present an opportunity for implementing variable seeding rate technology for soybean. These results emphasize potential benefits of increasing seeding rates in LYEs to capture more yield and decreasing seeding rates in MYEs and HYEs to reduce seed costs without penalizing yields and without exposing the crop to increased lodging and disease risks. Future studies looking at further identifying the main factors determining YEs influence on soybean AOPD responses will assist in defining more site-specific seeding rates within fields with the goal of improving overall farming profits. Adjustments on seeding rate prescription aiming the AOPD for each YE should consider the risks of stand losses during the season which could reduce the attainable plant density and final yields. As was shown in Fig. 2, especially in LYE, there is a large variability in seed yield at low plant densities and therefore a plant density under the AOPD will increase the probability of yield loss risk.

CONCLUSION

The most probable AOPD depended on the YE, with the plant density reduced by 24% in MYE–HYE relative to LYE. Decreasing plant density in the MYE–HYEs, when using above the AOPDs, will reduce potential yield losses related to yield-blocking factors such as lodging and disease issues and help farmers in seed savings.

To the extent of our knowledge, this is the first attempt to investigate the factors affecting the differential soybean seed yield response to plant density by YE. This study provides a new understanding highlighting that the reproductive ability of soybean, investigated via yield components, is the main factor driving changes in AOPD; and that differences in achieving the final plant density in each environment (relative to the target seeding rate) was not a decisive factor. Further research should be focused on identifying the main factors, considering soil, weather, and crop management, defining YEs to more accurately understand the overall soybean seed yield response to plant density and to assist farmers on improving the selection of the AOPDs for this crop.

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