Physiological Processes Leading to Similar Yield in Contrasting Soybean Maturity Groups

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ABSTRACT

Soybean [*Glycine max* (L.) Merr.] maturity groups (MGs) exhibit large variation in time to maturity, and are adapted to different latitudes. There is a range of MGs that have similar yield potential at most production regions, especially at temperate and tropical environments. We tested whether similar yields in contrasting MGs are achieved through different physiological processes. Our objectives were: (i) to characterize biomass accumulation, reproductive partitioning and seed set efficiency, and (ii) to analyze the role of N and radiation in biomass accumulation during the seed set period in contrasting MGs. Three MG III and V cultivars were tested in two growing environments. No significant yield or seed number differences were detected despite MG V had 20 d longer growth cycle. MG III had a longer seed set period (R1–R5), received more incident radiation during that period, and captured more N compared to the MG V. However, these cultivars had lower nitrogen use efficiency (NUE) (kg biomass per kg N uptake) and less radiation interception efficiency compared to MG V. These contrasting physiological processes determined similar biomass accumulation during R1 to R5. No differences between MGs were observed in biomass partitioning to reproductive structures and seed set efficiency during this period. Results showed contrasting MGs have different strategies for reaching similar yield, evidencing physiological processes that could be specifically tailored by breeders for either MG III (radiation interception efficiency, NUE) or MG V (duration of R1–R5 period, N uptake rate) cultivars for further yield increases.

Core Ideas

- Different soybean maturity groups are farmed in temperate regions with similar yields.
- A novel approach to understand yield formation in these groups is presented.
- Reproductive biology and biomass accumulation was essentially the same between groups.
- Groups differed in processes determining similar biomass accumulation during seed set.
- Yield limiting traits tailored for earlier and later soybean were identified.

SOYBEAN CULTIVARS are classified into MGs. The length of the cultivar growth cycle is controlled by nine major loci, and is regulated by temperature and photoperiod (Cober et al., 2001; Jiang et al., 2014). There are 13 MGs identified, from 000 to X. Each MG is specifically recommended to maximize yield at different latitudes; earlier maturity cultivars are commonly adapted to high latitudes and, inversely, later maturity ones are adapted to low latitudes (Zhang et al., 2007). However, at most production regions there is a range of possible MGs with similar attainable yields. Using a simulation model, Archontoulis et al. (2014) showed that for a given planting date and latitude there are some production regions with three to four MGs having similar yields. Similar findings are observed in field studies. For instance, in the central Argentina region farmers are using cultivars ranging from MG III to V with similar yield expectations (Baigorrí et al., 2002). With no water limitations in the mid-southern United States similar yields were reported by using MGs I, III, and V (Egli, 1993). Other examples were observed when comparing MG isolines ranging from IV to VI in Arkansas under adequate water supply (Mastrodomenico and Purcell, 2012).

Different mechanisms can explain the similar yield attained by contrasting MGs. Due to their longer growing cycle, later maturity cultivars capture more aboveground N and photosynthetic active radiation (PAR) at maturity compared to earlier ones in situations with minimized soil moisture stress (Egli, 1993; Jiang and Egli, 1995). Total biomass during the vegetative period is also higher for later maturity cultivars compared to earlier ones (Egli, 1993; Jiang and Egli, 1995). Edwards and Purcell (2005) showed no yield differences among MG II to VI under irrigated conditions, but the earlier ones had lower water requirements. More biomass produced at maturity, as a consequence of more N, PAR, and/or water capture available during normal seasons, is usually not correlated with yield since later cultivars have shown lower harvest index compared to early

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MGs (Schapaugh and Wilcox, 1980). While these reports study physiological processes at maturity, there is limited (Egli, 1993) information of possible differences during the seed set period (R1–R5) when comparing early and late maturity cultivars.

Physiological processes explaining yield can be described using different approaches. The most common describes yield variations associated with seed number determination per unit of land area, as this is the main numerical yield component (Board and Tan, 1995; Egli and Zhen-wen, 1991; Fischer, 2008). A mechanistic framework commonly used to explain seed number differences is the one proposed by Charles-Edwards (1984) and modified by Egli and Zhen-wen (1991) and Vega et al. (2001). This model formalizes the concept that seed number depends on physiological processes that occur between flowering (R1, Fehr and Caviness, 1977) and the beginning of seed growth (R5), known as the seed set period. This model is summarized as:

$$\text{Seed number} = \text{Bio}_{R1-R5} \times \text{PartCoef} \times \text{SetEff} \quad [1]$$

where Bio_{R1-R5} is total aboveground biomass accumulated from R1 to R5 (g m^{-2}), PartCoef is the proportion of total biomass partitioned to reproductive tissues during this period (g g^{-1}) and SetEff is the number of seeds set per unit of accumulated reproductive biomass (seed g^{-1}).

Biomass accumulation during the seed set period is limited by resource availability and genetic factors associated with resource uptake and use (Sinclair and Rufty, 2012). Biomass accumulation between R1 to R5 can be described in terms of N uptake and use using the following equation:

$$\text{Bio}_{R1-R5} = \text{Duration}_{R1-R5} \times \text{NupRate} \times \text{NUE} \quad [2]$$

where Duration_{R1-R5} is the number of days between R1 and R5, NupRate is the daily rate of N uptake (g N m^{-2} d^{-1}) and NUE is the N use efficiency for aboveground biomass production (kg biomass kg N^{-1}). The accumulation of biomass during the seed set period (Bio_{R1-R5}) can also be estimated as a function of radiation capture and use:

$$\text{Bio}_{R1-R5} = \text{PARinc}_{R1-R5} \times E_i \times \text{RUE} \quad [3]$$

where PARinc_{R1-R5} is the accumulated incident photosynthetic active radiation (MJ PAR m^{-2}) from R1 to R5, E_i is the radiation interception efficiency during the same period (fraction) and RUE is the radiation use efficiency for aboveground biomass production (g biomass MJ^{-1}).

A comprehensive study of these physiological processes in a set of cultivars differing in MG is currently lacking. Egli (1993) only focused on differences between MG III and V cultivars. He showed that these contrasting MGs had similar biomass accumulation and seed set efficiency. However, the study was based on only one cultivar per MG. Also, physiological components of biomass accumulation were not evaluated. Therefore, our general objective was to understand why contrasting MGs (III and V) currently used in the central Argentinean temperate region are attaining similar yields, focusing on physiological processes occurring during the seed set period. Specific objectives were: (i) to characterize biomass accumulation,

reproductive partitioning, and seed set efficiency during the period of seed number determination using the Charles-Edwards (1984) approximation, and (ii) to analyze the role of N and PAR capture and utilization in the accumulation of biomass during the seed set period. To test these ideas we evaluated three different cultivars per MG under field conditions.

MATERIALS AND METHODS
Experimental Details

Field experiments were conducted during the 2009/2010 and 2010/2011 growing seasons at Campo Experimental Villarino, located in Zavalla, Santa Fe, Argentina (33°1′ S, 60°53′ W). Soil type was a silty clay loam Vertic Argiudoll, Roldán series. Evaluated cultivars included three MG III (NK3400, NK3500, and NK3800, from Syngenta) and three MG V (NA5509, NA5909, and A5634, from Nidera). These cultivars are fully adapted to the experimental site latitude and are routinely grown in the region (Baigorrí et al., 2002). Planting date was 27 November in 2009/2010 and 16 December in 2010/2011. An analysis of planting dates from the last 5 yr in farmers' fields across the region shows that the experiment planting dates are within the 25 to 75% interquartile range for MGs including those evaluated in this experiment. Plots were four rows, 0.52 m apart, and 5.5 m long. Final plant population was adjusted to 38 plants m^{-2} after thinning at V1 (Fehr and Caviness, 1977). All measurements were taken from the two central rows. Weeds were chemically controlled initially and hand removed whenever necessary during the remaining of the season. Pests and diseases were controlled by spraying commercially recommended soybean products. Total rainfall during the growing seasons was 637 mm and 424 mm for 2009/2010 and 2010/2011, respectively. Specifically, from first flower appearance (R1) to beginning of seed filling (R5) rainfall was 121 and 199 mm for MG III in 2009/2010 and 2010/2011, respectively, and 216 and 132 mm for MG V in 2009/2010 and 2010/2011, respectively. Soil plant available water content at planting was determined gravimetrically until 200-cm depth using a soil probe. It was 228 and 239 mm for 2009/2010 and 2010/2011, respectively. Soybean was the previous crop in both years. Photoperiod, daily average temperatures, and the occurrence of phenological events for the MGs evaluated are described in Fig. 1.

Direct Measurement Variables

Timing of first flower appearance (R1), onset of pod development (R3), beginning of seed filling (R5), and physiological maturity (R7) were recorded at each plot every other day using 20 consecutive marked plants. The early reproductive period, defined from R1 to R5, was considered the seed set period. This period encompasses processes such as flower production, ovary fertilization, and pod abortion, determining the number of seeds set (Board and Tan, 1995; Egli and Zhen-wen, 1991; Jiang and Egli, 1995).

Total shoot biomass was hand-clipped at R1, R3, and R5 on 0.52 m^2 from the two central rows. A 0.25 m bordering section per row was maintained between sampling areas to avoid border effects. Samples collected at R5 were separated into reproductive (pods plus developing seeds) and vegetative (stem, leaves, and petioles) tissues, and dried at 60°C for 96 h before
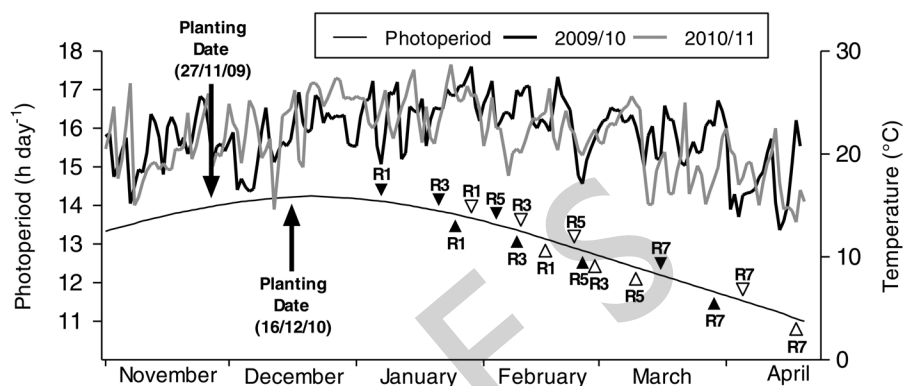
Fig. 1. Daily photoperiod from planting date to physiological maturity. Planting date for each season is described with arrows. Reproductive phenological stages are depicted for each maturity group and year. Points above the line represent average timings for 2009/2010 and points below the line represent average timings for 2010/2011. Full and empty symbols correspond to MG III and V, respectively. Temperature is daily mean temperature (°C) for 2009/2010 (black line) and for 2010/2011 (gray line).

dry weight was measured. Each sample was milled (1 mm) and total N was determined on a subsample using the Dumas method (Jung et al., 2003).

At physiological maturity plants from 1.04 m^2 area per plot from the two central rows were hand clipped, bagged, and dried. The samples were threshed and seeds weighed to calculate seed yield. Individual seed weight was calculated from a 200 seed subsample. Seed number per unit of land area was estimated as the ratio between crop yield and the individual seed dry weight.

Extraterrestrial radiation at the top of the atmosphere was obtained for our specific location and dates. It was converted to daily incident radiation using sunshine duration (hours), collected at a meteorological station located close (less 200 m) to the experiment, following the equation of Angström (1924) and local derived parameters (Ball et al., 2004). Sunshine duration was determined using a Campbell–Stokes sunshine recorder for considering the influence of cloudiness in total day irradiance. This method has been successfully used to estimate incident radiation for field studies (Edwards et al., 2005). Daily incident radiation was converted into photosynthetically active radiation (PAR$_{inc}$, MJ m^{-2} d^{-1}) by multiplying it by 0.5 (Monteith, 1965). Light interception efficiency (E$_i$, fraction) was estimated every 7 d on each plot from V5 until physiological maturity, as the ratio between light intercepted to light incidence. Light intercepted was the difference between one PAR measurement above the canopy (total light incidence) and the average of three PAR measurements immediately below green leaves (Purcell et al., 2002). Light measurements were taken with a 1 m linear radiometer (BAR-RAD 100, Cavadevices, Argentina) around noon on clear days. The sensor was fitted diagonally between the centers of two consecutive inter-rows.

Calculated Physiological Variables

Biomass accumulation between R1 to R5 (Bio$_{R1-R5}$, g m^{-2}) was calculated as the slope of the relationship between total biomass at R1, R3, and R5, and days after emergence. Partitioning to reproductive tissues (PartCoef, g g^{-1}) was calculated as the ratio between reproductive biomass at R5 and Bio$_{R1-R5}$. Seed set efficiency (SetEff, seed g^{-1}) was calculated as the ratio between final seed number and reproductive biomass at R5.

The number of days between R1 and R5 is Duration$_{R1-R5}$. Nitrogen uptake rate (NupRate, g N m^{-2} d^{-1}) was calculated as the slope of the relationship between N per square meter of land at R1, R3, and R5, and days. Nitrogen use efficiency for biomass production (NUE, kg biomass kg N^{-1}; Good et al., 2004) was calculated as the ratio between Bio$_{R1-R5}$ and total N uptake during the same period (Duration$_{R1-R5}$ × NupRate). This calculation determines a constant NUE for the R1 to R5 period. Single NUE estimations for each phenological stage would show NUE increases from R1 to R5. However, our intention here was to obtain an overall NUE for the period.

The integral incident PAR during R1 to R5 (PARinc$_{R1-R5}$, MJ m^{-2}) was calculated accumulating daily PAR$_{inc}$ during R1 to R5. Daily E$_i$ was estimated from weekly measurements by adjusting a logistic model ($R^2 > 0.9$) between measured E$_i$ and days after emergence. Daily PAR$_{int}$ was calculated as the product between daily PAR$_{inc}$ and daily E$_i$. Finally, intercepted PAR during R1 to R5 (PARint$_{R1-R5}$) was calculated by accumulating daily PAR$_{int}$ during the period. Light interception efficiency during R1 to R5 period (E$_i$, fraction) was calculated as the ratio between accumulated PARint$_{R1-R5}$ and accumulated PARinc$_{R1-R5}$. Radiation use efficiency (RUE, kg biomass kg MJ^{-1}) was calculated as the ratio between Bio$_{R1-R5}$ and PARint$_{R1-R5}$.

Experimental Design and Statistical Analysis

We used a randomized complete block design with three replicates. Evaluated factors were Year, Block nested within Year, MG, and Cultivar nested within MG along with the interactions with Year. A general linear ANOVA model was fitted using R software with package *agricolae* (R Development Core Team, 2008). The ANOVA assumptions, including residuals normality and homogeneity of variances were checked and no deviations were observed. The existence of alternative physiological processes will be demonstrated if contrasting MG effects are detected for physiological processes associated with yield determination. Post-hoc comparisons were conducted via the Fisher-protected least significant difference (LSD).

A cultivar-by-trait principal component analysis (PCA) was conducted using the GGE Biplot software (Yan and Rajcan, 2002) for visual examination of multiple trait relationships and cultivar comparison across physiological processes. Since physiological processes had different units, standardization was necessary before PCA (Yan and Rajcan, 2002). Correlation

between variables was estimated as the cosine of the angle formed by the two vectors, and can vary from -1 (maximum inverse correlation) to 1 (maximum positive correlation).

RESULTS

Phenological Stages Duration and Seed Yield

The duration of the vegetative period (days to R1) was closely associated with MG ($P \le 0.001$). Maturity group V had 20 d more vegetative period than MG III (Table 1). Time between R1 and R3 showed a different result; MG III cultivars had 3 d more than MG V cultivars for the R1 to R3 period ($P \le 0.01$). The duration of the R3 to R5 period showed a significant year × MG interaction. In year 2009/2010 no differences were detected between MGs (Table 1), but in 2010/2011 MG V exhibited a shorter period when compared to MG III. In spite of this interaction, MG III had almost 2 d longer R3 to R5

period compared to MG V ($P \le 0.01$). Total cycle length was significantly shorter in the second year due to the later planting date ($P \le 0.001$; Table 1). Days from planting to physiological maturity differed 20 d between MG III and V cultivars. Only minor differences among cultivars within MGs were observed.

As expected, seed yield was not significantly affected by MG, year or cultivar within MG (Table 1). Average yield for years, MGs, and cultivars was 3760 kg ha^{-1}. Cultivar yield was consistent between years, with no ranking changes. Therefore, results will focus on MG and cultivar main effects despite occasional significant year effects.

Seed Number, Biomass Accumulation, Reproductive Partitioning, and Seed Set Efficiency

Years differed in seed number per unit of land area (Table 2). The higher seed number observed for 2010/2011 was associated with a reduction in seed size (data not shown), resulting

Table 1. Growth stages duration and seed yield for years, maturity groups (MGs) and cultivars within MGs. Values are averages of three replicates. Mean values for each year, MG, cultivars, and their interaction are displayed. Percentage of variation are represented by sums of square (% SS) for each source of variation.

Year	Maturity group	Cultivar	Days to R1	Days between R1 and R3	Days between R3 and R5	Physiological maturity	Grain yield
			——————————————————— d ———————————————————				kg ha^{-1}
2009/2010			52.0 ± 2.7	11.9 ± 0.5	14.6 ± 0.6	119.2 ± 2.4	3710 ± 80
2010/2011			50.1 ± 2.6	13.8 ± 0.7	12.7 ± 0.8	112.9 ± 2.4	3807 ± 106
	III		40.3 ± 0.4	14.2 ± 0.5	14.6 ± 0.4	106.2 ± 0.8	3818 ± 111
	V		61.8 ± 0.5	11.6 ± 0.6	12.8 ± 0.9	125.8 ± 0.7	3699 ± 72
2009/2010	III		41.0 ± 0.2	13.7 ± 0.2	13.8 ± 0.3	109.3 ± 0.3	3807 ± 84
	V		63.0 ± 0.3	10.1 ± 0.4	15.4 ± 0.8	129.0 ± 0.0	3614 ± 73
2010/2011	III		39.6 ± 0.5	14.7 ± 0.7	15.6 ± 0.3	103.1 ± 0.4	3829 ± 137
	V		60.6 ± 0.5	13.0 ± 0.5	10.1 ± 0.5	122.7 ± 0.2	3784 ± 70
2009/2010	III	NK 3400	41.0 ± 0.0	13.7 ± 0.3	14.0 ± 1.0	110.6 ± 0.7	3735 ± 86
		NK 3500	41.3 ± 0.3	13.3 ± 0.3	12.7 ± 0.3	108.0 ± 0.0	4143 ± 178
		NK 3800	41.3 ± 0.7	14.0 ± 0.6	14.7 ± 0.9	109.3 ± 0.7	3550 ± 198
	V	A 5634RG	64.0 ± 0.6	9.7 ± 0.9	14.0 ± 1.2	129.0 ± 0.0	3604 ± 334
		NA 5509RG	63.0 ± 0.0	9.0 ± 1.0	19.0 ± 1.7	129.0 ± 0.0	3619 ± 47
		NA 5909RG	62.0 ± 1.0	11.7 ± 0.9	13.3 ± 0.7	129.0 ± 0.0	3619 ± 112
2010/2011	III	NK 3400	40.3 ± 0.7	14.7 ± 0.7	15.3 ± 0.7	104.0 ± 1.2	4370 ± 427
		NK 3500	41.0 ± 0.0	12.3 ± 1.7	16.5 ± 0.4	102.6 ± 1.3	3519 ± 219
		NK 3800	37.3 ± 1.7	17.0 ± 2.1	15.3 ± 0.7	102.6 ± 0.7	3598 ± 55
	V	A 5634RG	61.3 ± 0.7	11.7 ± 1.5	8.7 ± 0.9	122.0 ± 0.6	3598 ± 81
		NA 5509RG	61.3 ± 1.3	13.3 ± 1.8	10.3 ± 0.7	123.0 ± 0.0	3978 ± 219
		NA 5909RG	59.0 ± 1.0	14.0 ± 0.0	11.3 ± 1.5	123.0 ± 0.0	3778 ± 166

Source of variation	P value (LSD)	% SS	P value (LSD)	% SS	P value (LSD)	% SS	P value (LSD)	% SS	P value (LSD)	% SS
Year	***(1.1)†	1	*(1.5)	21	**	12	***(0.2)	9	ns‡	3
Block (Year)	ns	0	ns	4	ns	3	ns	0	ns	9
MG	***(1.1)	98	**(1.5)	38	**	11	***(0.2)	90	ns	5
Year × MG	ns	0	ns	5	***(2.1)	44	ns	0	ns	2
Cultivar (MG)	*(1.9)	1	ns	24	*	14	*(0.3)	1	ns	31
Year × Cultivar (MG)	ns	0	ns	10	*(3.6)	16	ns	0	ns	50

* $P \le 0.05$.

** $P \le 0.01$.

*** $P \le 0.001$.

† Least significant difference (LSD) for $P \ge 0.05$.

‡ ns, not significant at $P \ge 0.05$.

in no yield difference between seasons. Seed number per unit of land area was not significantly different across MGs (Table 2, $P \geq 0.05$); MG III cultivars had ~2800 seeds m^{-2} while MG V cultivars had ~2700 seeds m^{-2}. There was a significant year × MG interaction accounting for 7% sum of squares for seed number (Table 2). This interaction was associated with the MG III having more seed number in year 2010/2011 compared to year 2009/2010 (Table 2). Most of this interaction is explained by NK3400 having a greater seed number than the other MG III cultivars (cultivar main effect).

Total biomass accumulation during the seed set period (R1–R5), reproductive partitioning, and seed set efficiency were affected by the growing season (Table 2). There were no significant differences in biomass accumulation between both MGs (Table 2, $P \geq 0.05$). On average, plant biomass accumulation during this period was 330 g m^{-2}. Reproductive partitioning coefficient of accumulated biomass was not significantly

different for the MGs evaluated (average PartCoeff 0.23). Seed set efficiency was not significantly different between MGs (Table 2, $P \geq 0.05$). Both MGs set ~40 seeds per unit of accumulated reproductive biomass at R5. When analyzing cultivar effects within each MG, differences were observed for SetEff only (Table 2).

Nitrogen Uptake and Use during Seed Set Period

The duration of the seed set period from R1 to R5 was similar for both years (Table 3). This period was 5 d longer for MG III cultivars compared to MG V ones (Table 3, $P \leq 0.001$). Maturity group III captured 30% more N per day compared to the MG V cultivars and significant differences among cultivars within each MG were also found (Table 3, $P \leq 0.05$). For example, NupRate of cultivar NK3800 was similar to some of the MG V cultivars. Maturity groups were consistently different in NupRate even though cultivar and year by MG effects were

Table 2. Seed number, biomass accumulation from R1 to R5, reproductive partitioning coefficient and seed set efficiency for years, maturity groups (MG) and cultivars within maturity groups. Values are averages of three replicates. Mean values for each year, MG, cultivars, and their interaction are displayed. Percentage of variation are represented by sums of square (% SS) for each source of variation.

Year	Maturity group	Cultivar	Seed number	Biomass accumulation$_{R1–R5}$	Reproductive partitioning coefficient	Seed set efficiency
			no. m^{-2}	g m^{-2}	g g^{-1}	seeds g^{-1}
2009/2010			2678 ± 58	292 ± 16	0.20 ± 0.01	48 ± 2
2010/2011			2919 ± 114	369 ± 29	0.28 ± 0.01	31 ± 2
	III		2884 ± 121	356 ± 23	0.22 ± 0.01	40 ± 2
	V		2712 ± 51	304 ± 25	0.25 ± 0.01	40 ± 3
2009/2010	III		2642 ± 64	320 ± 9	0.18 ± 0.01	47 ± 2
	V		2713 ± 53	263 ± 19	0.23 ± 0.01	50 ± 3
2010/2011	III		3126 ± 140	397 ± 31	0.27 ± 0.01	32 ± 2
	V		2711 ± 52	345 ± 28	0.28 ± 0.01	31 ± 2
2009/2010	III	NK3400	2700 ± 55	290 ± 20	0.18 ± 0.01	52 ± 1
		NK3500	2819 ± 154	348 ± 27	0.21 ± 0.01	40 ± 3
		NK3800	2407 ± 161	322 ± 10	0.15 ± 0.00	49 ± 5
	V	A5634	2642 ± 217	264 ± 82	0.18 ± 0.02	64 ± 7
		NA5509	2818 ± 102	282 ± 19	0.23 ± 0.01	44 ± 3
		NA5909	2680 ± 47	243 ± 33	0.27 ± 0.03	42 ± 2
2010/2011	III	NK3400	3733 ± 396	509 ± 32	0.22 ± 0.02	34 ± 3
		NK3500	2958 ± 103	377 ± 50	0.28 ± 0.03	28 ± 6
		NK3800	2688 ± 89	296 ± 77	0.30 ± 0.03	33 ± 6
	V	A5634	2673 ± 156	293 ± 69	0.29 ± 0.03	34 ± 6
		NA5509	2783 ± 148	377 ± 61	0.28 ± 0.03	28 ± 4
		NA5909	2677 ± 125	366 ± 91	0.28 ± 0.04	30 ± 6

Source of variation	P value	% SS	P value	% SS	P value	% SS	P value	% SS
Year	*(215)†	14	*(68)	27	**(0.03)	51	***(5)	61
Block (Year)	ns‡	5	ns	13	ns	4	ns	7
MG	ns	15	ns	14	ns	9	ns	0
Year × MG	*(305)	7	ns	18	ns	2	ns	0
Cultivar (MG)	*(373)	39	ns	0	ns	11	*(9)	24
Year × Cultivar (MG)	ns	19	ns	28	ns	22	ns	6

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

† Least significant difference (LSD) for $P \geq 0.05$.

‡ ns, not significant at $P \geq 0.05$.

Table 3. Duration from R1 to R5, N uptake rate from R1 to R5 and N use efficiency for years, maturity groups (MGs) and cultivars within MGs. Values are averages of three replicates. Mean values for each year, MG, cultivars, and their interaction are displayed. Percentage of variation are represented by sums of square (% SS) for each source of variation.

Year	Maturity group	Cultivar	Duration$_{R1-R5}$	Nitrogen uptake rate$_{R1-R5}$	Nitrogen use efficiency$_{R1-R5}$
			d	g d^{-1}	g g^{-1}
2009/2010		.	27 ± 1	0.25 ± 0.02	46 ± 2
2010/2011			27 ± 1	0.36 ± 0.03	39 ± 2
	III		29 ± 1	0.34 ± 0.03	37 ± 1
	V		24 ± 1	0.26 ± 0.02	48 ± 2
2009/2010	III		27 ± 0	0.29 ± 0.08	41 ± 1
	V		26 ± 1	0.20 ± 0.01	51 ± 2
2010/2011	III		30 ± 1	0.40 ± 0.03	33 ± 0
	V		23 ± 1	0.32 ± 0.09	45 ± 1
2009/2010	III	NK3400	28 ± 1	0.24 ± 0.04	44 ± 4
		NK3500	26 ± 1	0.37 ± 0.05	37 ± 2
		NK3800	29 ± 1	0.27 ± 0.02	41 ± 2
	V	A5634	24 ± 0	0.20 ± 0.03	53 ± 7
		NA5509	28 ± 1	0.20 ± 0.02	51 ± 3
		NA5909	25 ± 1	0.21 ± 0.03	48 ± 7
2010/2011	III	NK3400	30 ± 0	0.52 ± 0.02	33 ± 1
		NK3500	28 ± 2	0.43 ± 0.03	31 ± 0
		NK3800	32 ± 2	0.26 ± 0.06	34 ± 1
	V	A5634	20 ± 1	0.31 ± 0.05	46 ± 4
		NA5509	24 ± 1	0.37 ± 0.02	42 ± 2
		NA5909	25 ± 1	0.26 ± 0.08	49 ± 2

Source of variation			P value	% SS	P value	% SS	P value	% SS
Year			ns†	0	***(0.05)	32	**(5)	24
Block (Year)			ns	2	ns	4	ns	3
MG			***(1)‡	51	**(0.05)	19	***(5)	62
Year × MG			**(1)	17	ns	0	ns	1
Cultivar (MG)			*(1)	25	*(0.08)	22	ns	5
Year × Cultivar (MG)			ns	6	*(0.12)	22	ns	5

* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.
† ns, not significant at $P \geq 0.05$.
‡ Least significant difference (LSD) for $P \geq 0.05$.

observed. Cultivars MG V showed a 30% more NUE for biomass production compared to MG III ones (Table 3, $P \leq 0.001$).

The duration of the R1 to R5 period represented 27 and 19% of total cycle from planting to maturity in MG III and V, respectively (Fig. 2a). Nitrogen accumulated during the same period represented 37 and 21% of total N captured from planting to maturity for MG III and V, respectively.

Photosynthetic Active Radiation Interception and Use Efficiency during the Seed Set Period

Accumulated incident PAR during R1 to R5 was not significantly different between years (Table 4). Maturity group III cultivars were exposed to almost 40% more accumulated incident PAR during the R1 to R5 period compared to MG V cultivars (Table 4). This increased incident PAR was related with different R1 to R5 period duration (Table 2) and moment of occurrence.

Light interception was higher in 2009/2010 compared to 2010/2011 (Table 4). Maturity group III cultivars intercepted 78% of the 341 MJ m^{-2} of PAR$_{inc}$ during the seed set period, and MG V cultivars intercepted 92% of 244 MJ m^{-2} of PAR$_{inc}$ (Table 4). The 40% difference in PAR availability favoring MG III was translated in only 18% more PAR$_{int}$ due to differences in E_i. Radiation use efficiency was not different between MG cultivars, but was higher in the 2010/2011 growing season (Table 4).

Of the total PAR intercepted from planting to physiological maturity, MG III cultivars captured almost 40% during the R1 to R5 period (Fig. 2b). Maturity group V cultivars captured slightly less than 30% of the total intercepted PAR during the R1 to R5 period.

Physiological Strategies Associated with Maturity Groups

A principal component analysis for cultivars and those physiological processes that were significantly different between MGs (Duration$_{R1-R5}$, NUE, PARinc$_{R1-R5}$, E_i, and NupRate) was conducted for synthetizing differences in yield determination processes associated with MGs (Fig. 3).

Table 4. Accumulated incident photosynthetically active radiation (PAR), interception efficiency, and radiation use efficiency from R1 to R5 for years, maturity groups (MGs) and cultivars within MGs. Values are averages of three replicates. Mean values for each year, MG, cultivars, and their interaction are displayed. Percentage of variation are represented by sums of square (% SS) for each source of variation.

Year	Maturity group	Cultivar	Accumulated incident PAR$_{R1-R5}$	Light interception efficiency	Radiation use efficiency$_{R1-R5}$
			MJ m^{-2}		g MJ^{-1}
2009/2010			290 ± 13	0.91 ± 0.02	1.13 ± 0.06
2010/2011			292 ± 14	0.80 ± 0.02	1.60 ± 0.11
	III		341 ± 6	0.78 ± 0.02	1.35 ± 0.09
	V		244 ± 7	0.92 ± 0.01	1.36 ± 0.11
2009/2010	III		340 ± 3	0.84 ± 0.01	1.13 ± 0.04
	V		240 ± 6	0.97 ± 0.00	1.13 ± 0.08
2010/2011	III		342 ± 9	0.71 ± 0.02	1.61 ± 0.10
	V		248 ± 9	0.87 ± 0.01	1.59 ± 0.11
2009/2010	III	NK3400	341 ± 3	0.82 ± 0.06	1.05 ± 0.22
		NK3500	330 ± 4	0.88 ± 0.01	1.20 ± 0.11
		NK3800	349 ± 11	0.82 ± 0.03	1.13 ± 0.07
	V	A5634	218 ± 5	0.98 ± 0.01	1.23 ± 0.36
		NA5509	267 ± 11	0.96 ± 0.01	1.11 ± 0.07
		NA5909	236 ± 14	0.98 ± 0.01	1.05 ± 0.15
2010/2011	III	NK3400	332 ± 4	0.76 ± 0.01	2.01 ± 0.09
		NK3500	315 ± 10	0.74 ± 0.03	1.63 ± 0.23
		NK3800	369 ± 28	0.64 ± 0.04	1.21 ± 0.17
	V	A5634	213 ± 20	0.87 ± 0.02	1.62 ± 0.41
		NA5509	256 ± 17	0.89 ± 0.01	1.62 ± 0.17
		NA5909	275 ± 14	0.86 ± 0.02	1.53 ± 0.34

Source of variation	P value	% SS	P value	% SS	P value	% SS
Year	ns†	0	***(0.03)	32	**(0.30)	56
Block (Year)	ns	1	ns	2	ns	13
MG	***(4)‡	85	**(0.03)	55	ns	0
Year × MG	ns	0	ns	0	ns	0
Cultivar (MG)	*(13)	11	ns	6	ns	14
Year × Cultivar (MG)	ns	3	ns	5	ns	17

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

† ns, not significant at $P \geq 0.05$.

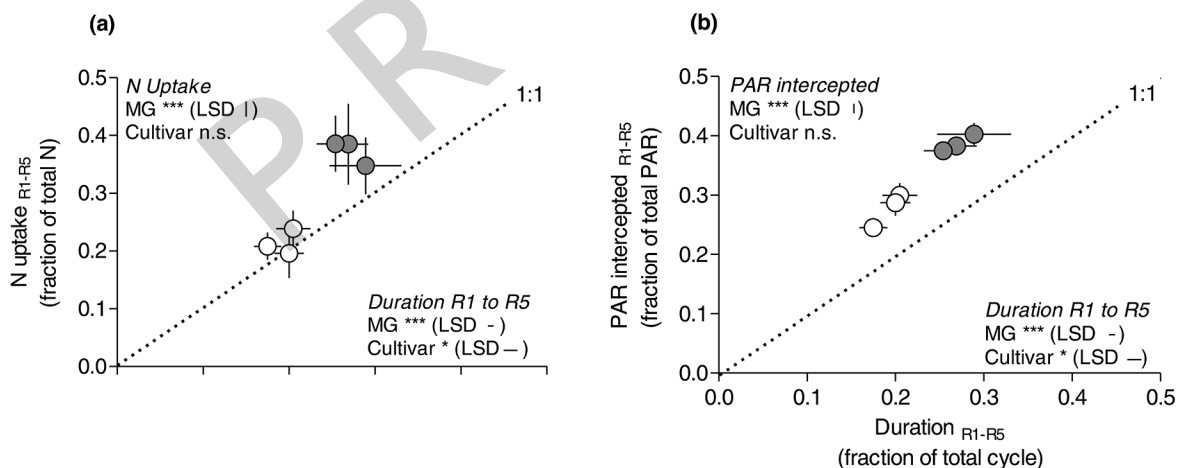‡ Least significant difference (LSD) for $P \geq 0.05$.

Fig. 2. Relationship between (a) N and (b) radiation captured during the R1 to R5 period and duration of this same period. Gray and white symbols represents III and V maturity groups, respectively. Values are averages between years. Horizontal and vertical bars indicate LSD ($P \leq 0.05$). Icons *, *** indicate significant differences at 0.05, 0.001 probably level, respectively; ns means nonsignificant.
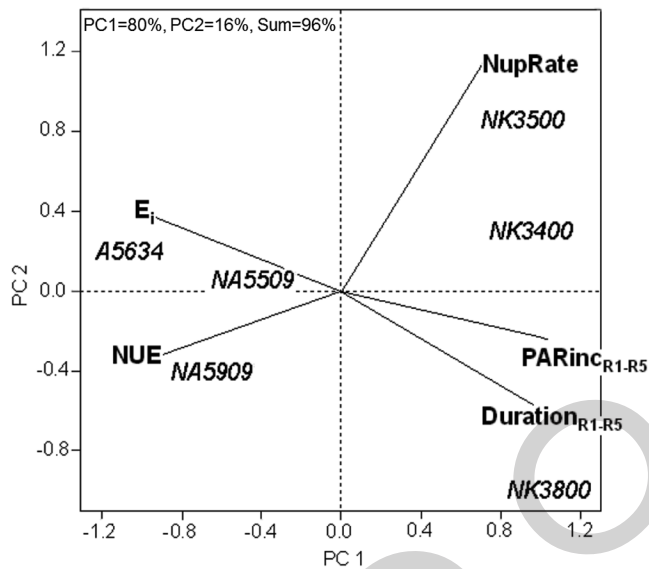
Fig. 3. Bi-plot of first and second principal components for III and V maturity group cultivars. Physiological processes are represented as black lines. NUE is nitrogen use efficiency, E_i is photosynthetic active radiation (PAR) interception efficiency, NupRate is the nitrogen uptake rate, $PARinc_{R1-R5}$ is photosynthetic active radiation incident, all of this between R1 to R5 and $Duration_{R1-R5}$ is duration of seed set period. Percentage of variation explained by each principal component (PC) is detailed oat the upper left of the figure. Cultivars NK3400, NK3500, and NK3800 are MG III, and NA5509, NA5909, and A5634 are MG V.

Both MGs evaluated were grouped along the first principal component. Maturity group V cultivars were clustered with high NUE and E_i. Maturity group III cultivars showed higher NupRate, $PARinc_{R1-R5}$, and $Duration_{R1-R5}$ than MG V cultivars. However, some cultivars within MG III differed in some of these associations. For example, NK3800 exhibits the highest $Duration_{R1-R5}$, NK3500 the greatest NupRate and NK3400 was intermediate (Fig. 3). The highest $PARinc_{R1-R5}$ was positively related with the $Duration_{R1-R5}$ in the case of MG III cultivars and negatively associated with E_i. The negative correlations that can be observed for contrasting MGs between NupRate and NUE, and between E_i and $PARinc_{R1-R5}$ (or $Duration_{R1-R5}$), are evidencing alternative physiological processes for biomass accumulation.

DISCUSSION

Maturity groups III and V had on average similar seed number determined during R1 to R5, biomass accumulation during this period, reproductive partitioning, and seed set efficiency. However, they differed in the physiological processes leading to biomass accumulation during the seed set period. Maturity group III cultivars had larger N uptake rate while MG V ones had higher N use efficiency. In terms of radiation capture during the seed set period, MG III cultivars had more PAR accumulated during the seed set period, while MG V ones had larger interception efficiency. These physiological processes led to similar biomass accumulation during the period of seed number determination (R1–R5). Given the similarities in reproductive biology of these contrasting MGs, this also resulted in equivalent yield. This characterization highlights specific physiological processes to be improved in both MGs. For instance, increasing N uptake rate in MG V cultivars while increasing NUE in MG III ones.

The reproductive processes controlling seed number (Eq. [1]) were similar between MGs. Reproductive partitioning during the seed set period was ~23%, and was not different between MGs III and V. This trait is known to be cultivar dependent and stable across diverse environmental and management conditions (Egli et al., 1985). Even though cultivar variation exists among high yielding cultivars from Argentina and United States (Rotundo et al., 2012), the results from the present study show that the variation in reproductive partitioning is not associated with MGs, at least when comparing between MGs III and V. Seed set efficiency is also considered a trait having a strong genetic component (Egli and Zhen-wen, 1991). Variation in seed set efficiency was also observed in a screening of high yielding cultivars from Argentina and United States (Rotundo et al., 2012), and our results are also indicating this variation was not related to maturity groups.

Nitrogen accumulation is strongly related with soybean yield (Salvagiotti et al., 2008; Rotundo et al., 2014). Maturity group III captured more total aboveground N from R1 to R5 mostly due to faster absorption rate and a 20% longer seed set period compared to MG V. Late cultivars compensated for slower rates of N capture by a higher NUE. Possible mechanisms responsible of the observed trade-off, however, are not clear. Nitrogen uptake rate and NUE can be associated with N_2 fixation rates. For example, George and Singleton (1992) found a positive relationship between N uptake rate and N_2 fixation. On the other hand, Andrews et al. (2009) showed that N_2 fixation has a higher energetic cost compared to mineral N acquisition. This would indicate a negative relationship between N_2 fixation and NUE. Both antecedents suggest a role of N_2 fixation in explaining negative associations between NUE and NupRate. Divito et al. (2016) showed that early MGs had a higher leaf to stem ratio during the seed set period when compared to late MGs. Since N uptake largely depends on internal plant regulation (Gastal and Lemaire, 2002) having increased proportion of N rich tissues (e.g., leaves) may promote higher N uptake rates in earlier MGs.

Maturity group III cultivars had more PAR availability during the seed set period compared to MG V. This difference was related to two factors. First, the duration of the R1 to R5 period was longer for MG III. Second, the shorter vegetative period of MG III cultivars places the R1 to R5 period in a moment with higher irradiance compared to MG V cultivars (11.6 MJ PAR m^{-2} per day for MG III vs. 10.2 MJ PAR m^{-2} per day for MG V). Cooper (2003) reported that earlier flowering resulted in higher potential yields due to high irradiance during reproductive stages. This second factor poses a drawback for comparing biomass accumulation during the R1 to R5 period since this period actually occurs at different calendar days, exposing it to potentially different environmental conditions other than radiation (Egli, 1994). However, environmental conditions in terms of temperature and rainfall did not differ substantially between MGs seed set period (mean temperature: 23.9 vs. 23.1°C for MGs III and V, respectively; averaged rainfall: 160 vs. 132 mm for MGs III and V, respectively). Another indication that environmental conditions during the seed set period for both MGs were only slightly different was that similar RUE was observed between MGs (~1.4 g d^{-1} MJ^{-1}). Meaningful variation in RUE would have indicated substantial variation in PAR intensity due to

the negative correlation frequently observed between RUE and PAR intensity (Van Roekel and Purcell, 2014).

The result that duration of the R1 to R5 period was longer in MG III compared to MG V, detected in 2010/2011, was intriguing since it would have been expected the opposite. For checking this result, an empirical model developed in Argentina to predict the occurrence of phenological events in soybean was used (Peltzer and Peltzer, 2013). The duration of R2 to R5 for five MG III cultivars and five MG V cultivars was estimated for our planting dates in 2009/2010 and 2010/2011. For 2009/2010, the duration of the early reproductive phase (R2–R5) was 30 d for MG III and 25 d for MG V. For 2010/2011, the duration was 28 d for MG III and 20 d for MG V. In 2009/2010 the average photoperiod from R1 to R5 was 14.0 and 13.3 hs for MG III and V, respectively. In 2010/2011 it was 13.4 and 12.8 h for MG III and V, respectively (Fig. 1). Based on this small difference in photoperiod it would have been expected MG V having a longer R1 to R5 period duration, which was not the case. Observing the results reported by Archontoulis et al. (2014) it is evident that there is substantial variation in the duration of the period from R1 to R5 within MGs III and V, where some MG III cultivars had a longer R1 to R5 period than specific MG V cultivars.

Two different strategies of resource capture and use leading to similar yield were detected. The principal component analysis showed physiological processes that were associated with MGs evaluated, and these results help to identify physiological processes with possibilities of increasing yield that are specially tailored for either III or V MGs. There is no information related to the degree of independence among these processes due to biophysical constraints and/or genetic linkage. Assuming no biophysical or genetic trade-offs among physiological processes, if NUE of MG III cultivars could be increased to that of the MG V (48 g g^{-1}), maintaining constant all the others parameters of the model, seed number and yield could increase up to 44%. For MG V, the main yield limitation can be ascribed to its relatively short seed set period. This relatively short seed set period determined that only 20% of total N and 27% of PAR were capture and translated into biomass accumulation during this important period. There is evidence that manipulating photoperiod after flowering can increase the duration of the seed set period (Kantolic and Slafer, 2001, 2005). Thereby, selecting for low photoperiodic sensitivity before R1 and high photoperiodic sensitivity after R1 could help create cultivars with a longer reproductive period without affecting total crop cycle duration (Kantolic et al., 2007). A 5 d longer seed set period in MG V cultivars could determine 20% more N and PAR capture, representing 44 and 36% more seeds and yield, respectively, maintaining constant all the others parameters of the model. These examples are showing the value of our characterization identifying physiological processes that can potentially increase yield in a particular MG.

CONCLUSIONS

Farmers in temperate regions commonly use a range of MGs, which in our production system ranges from MGs III to V. No significant differences in seed number per unit of land area, reproductive biomass partitioning, and seed set efficiency during the R1 to R5 period were evident for these contrasting MGs. They also showed similar biomass accumulation during the R1 to R5 period. However, they differed in their physiological strategies leading for this similar biomass accumulation, evidencing different physiological processes during R1 to R5. Maturity group III cultivars had more N uptake rate and incident radiation during this period. Maturity group V cultivars had more NUE and radiation interception efficiency.

From an applied perspective our analysis allowed the identification of specific yield limiting physiological processes for both MGs III and V. Maturity group III was limited by light interception during the seed set period, so agronomic practices like narrower row spacing or increased plant populations could help increase their yields. Given adequate phenotyping protocols breeding for particular physiological processes related to N uptake and use efficiency, or PAR interception efficiency, can help increase yields at specific MGs.

REFERENCES

Andrews, M., P.J. Lea, J.A. Raven, and R.A. Azevedo. 2009. Nitrogen use efficiency. 3. Nitrogen fixation: Genes and costs. Ann. Appl. Biol. 155:1–13. doi:10.1111/j.1744-7348.2009.00338.x

Angström, A. 1924. Solar and terrestrial radiation. Quart. J. Roy. Met. Soc. 50:121–126. doi:10.1002/qj.49705021008

Archontoulis, S.V., F.E. Miguez, and K.J. Moore. 2014. A methodology and an optimization tool to calibrate phenology of short-day species included in the APSIM PLANT model: Application to soybean. Environ. Model. Softw. 62:465–477. doi:10.1016/j.envsoft.2014.04.009

Baigorrí, H.E., C. Ghida Daza, M. Cuniberti, R. Herrero, J. Aragón, S. Vallone et al. 2002. Evolución y perspectivas de la producción y de la investigación en soja en Argentina. (In Spanish, with English abstract.) In: Anais do II Congresso Brasileiro de Soja e Mercosoja, Foz do Iguaçu PR Brasil. 2–6 June 2002. EMBRAPA, Londrina, PR, Brazil. p. 84–95.

Ball, R.A., L.C. Purcell, and S.K. Carey. 2004. Evaluation of solar radiation prediction models in North America. Agron. J. 96:391–397. doi:10.2134/agronj2004.0391

Board, J.E., and Q. Tan. 1995. Assimilatory capacity effects on soybean yield components and pod number. Crop Sci. 35:846–851. doi:10.2135/cropsci1995.0011183X003500030035x

Charles-Edwards, D.A. 1984. On the ordered development of plants 1. An hypothesis. Ann. Bot. (Lond.) 53:699–707.

Cober, E.R., D.W. Stewart, and H.D. Voldeng. 2001. Photoperiod and temperature responses in early-maturing, near-isogenic soybean lines. Crop Sci. 41:721–727. doi:10.2135/cropsci2001.413721x

Cooper, R.L. 2003. A delayed flowering barrier to higher soybean yield. Field Crops Res. 82:27–35. doi:10.1016/S0378-4290(03)00003-0

Divito, G.A., H.E. Echeverría, F.H. Andrade, and V.O. Sadras. 2016. Soybean shows an attenuated nitrogen dilution curve irrespective of maturity group and sowing date. Field Crops Res. 186:1–9. doi:10.1016/j.fcr.2015.11.004

Edwards, J.T., and L.C. Purcell. 2005. Soybean yield and biomass responses to increasing plant population among diverse maturity groups: I. Agronomic characteristics. Crop Sci. 45:1770–1777. doi:10.2135/cropsci2004.0564

Edwards, J.T., L.C. Purcell, and D.E. Karcher. 2005. Soybean yield and biomass responses to increasing plant population among diverse maturity groups: II. Light interception and utilization. Crop Sci. 45:1778–1785. doi:10.2135/cropsci2004.0570

Egli, D.B. 1993. Cultivar maturity and potential yield of soybean. Field Crops Res. 32:147–158. doi:10.1016/0378-4290(93)90027-K

Egli, D.B. 1994. Cultivar maturity and reproductive growth duration in soybean. J. Agron. Crop Sci. 173:249–254. doi:10.1111/j.1439-037X.1994.tb00561.x

Egli, D.B., R.D. Guffy, and J.E. Leggett. 1985. Partitioning of assimilate between vegetative and reproductive growth in soybean. Agron. J. 77:917–922. doi:10.2134/agronj1985.00021962007700060020x

Egli, D.B., and Y. Zhen-wen. 1991. Crop growth rate and seeds per unit area in soybean. Crop Sci. 31:439–442. doi:10.2135/cropsci1991.0011183X003100020043x

Fehr, W.R., and C.E. Caviness. 1977. Stages of soybean development. Spec. Rep. 80. Iowa Agric. and Home Economics Exp. Stn., Ames. p. 3–11.

Fischer, R.A. 2008. The importance of grain or kernel number in wheat: A reply to Sinclair and Jamieson. Field Crops Res. 105:15–21. doi:10.1016/j.fcr.2007.04.002

Gastal, F., and G. Lemaire. 2002. N uptake and distribution in crops: An agronomical and ecophysiological perspective. J. Exp. Bot. 53:789–799. doi:10.1093/jexbot/53.370.789

George, T., and P.W. Singleton. 1992. Nitrogen assimilation traits and dinitrogen fixation in soybean and common bean. Agron. J. 84:1020–1028. doi:10.2134/agronj1992.00021962008400060022x

Good, A.G., A.K. Shrawat, and D.G. Muench. 2004. Can less yield more? Is reducing nutrient input into the environment compatible with maintaining crop production? Trends Plant Sci. 9:597–605. doi:10.1016/j.tplants.2004.10.008

Jiang, H., and D.B. Egli. 1995. Soybean seed number and crop growth rate during flowering. Agron. J. 87:264–267. doi:10.2134/agronj1995.00021962008700020020x

Jiang, B., H. Nan, Y. Gao, L. Tang, Y. Yue, S. Lu et al. 2014. Allelic combinations of soybean maturity loci E1, E2, E3 and E4 result in diversity of maturity and adaptation to different latitudes. PLoS One 9:e106042. doi:10.1371/journal.pone.0106042

Jung, S., D.A. Rickert, N.A. Deak, E.D. Aldin, J. Recknor, L.A. Johnson, and P.A. Murphy. 2003. Comparison of Kjeldahl and Dumas methods for determining protein contents of soybeans products. J. Am. Oil Chem. Soc. 80:1169–1173. doi:10.1007/s11746-003-0837-3

Kantolic, A.G., J.L. Mercau, G.A. Slafer, and V.O. Sadras. 2007. Simulated yield advantages of extending post-flowering development at the expense of a shorter pre-flowering development in soybean. Field Crops Res. 101:321–330. doi:10.1016/j.fcr.2006.12.008

Kantolic, A.G., and G.A. Slafer. 2001. Photoperiod sensitivity after flowering and seed number determination in indeterminate soybean cultivars. Field Crops Res. 72:109–118. doi:10.1016/S0378-4290(01)00168-X

Kantolic, A.G., and G.A. Slafer. 2005. Reproductive development and yield components in indeterminate soybean as affected by post-flowering photoperiod. Field Crops Res. 93:212–222. doi:10.1016/j.fcr.2004.10.001

Mastrodomenico, A., and L.C. Purcell. 2012. Soybean nitrogen fixation and nitrogen remobilization during reproductive development. Crop Sci. 52:1281–1289. doi:10.2135/cropsci2011.08.0414

Monteith, J.L. 1965. Light distribution and photosynthesis in field crops. Ann. Bot. (Lond.) 29:17–37.

Peltzer, H.F., and N.G. Peltzer. 2013. Modelo de simulación de fenología de soja (SI.FE.SOJA): Una herramienta útil para evitar el estrés hídrico durante el periodo crítico. p. 155–160. In: Congreso Argentino de AgroInformática, Córdoba, Argentina. 16–20 September. Soc. Argentina de Informática e Investigación Operativa, Buenos Aires, Argentina.

Purcell, L.C., R.A. Ball, J.D. Reaper, and E.D. Vories. 2002. Radiation use efficiency and biomass production in soybean at different plant population densities. Crop Sci. 42:172–177. doi:10.2135/cropsci2002.0172

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org (accessed ?).

Rotundo, J.L., L. Borrás, J. De Bruin, and P. Pedersen. 2012. Physiological strategies for seed number determination in soybean: Biomass accumulation, partitioning and seed set efficiency. Field Crops Res. 135:58–66. doi:10.1016/j.fcr.2012.06.012

Rotundo, J.L., L. Borrás, J. De Bruin, and P. Pedersen. 2014. Soybean nitrogen uptake and utilization in Argentina and United States cultivars. Crop Sci. 54:1153–1165. doi:10.2135/cropsci2013.09.0618

Salvagiotti, F., K.G. Cassman, J.E. Specht, D.T. Walters, A. Weiss, and A. Dobermann. 2008. Nitrogen uptake, fixation and response to fertilizer N in soybeans: A review. Field Crops Res. 108:1–13. doi:10.1016/j.fcr.2008.03.001

Schapaugh, W.T., Jr., and J.R. Wilcox. 1980. Relationships between harvest indices and other plant characteristics in Soybeans. Crop Sci. 20:529–533. doi:10.2135/cropsci1980.0011183X002000040028x

Sinclair, T.R., and T.W. Rufty. 2012. Nitrogen and water resources commonly limit crop yield increases, not necessarily plant genetics. Glob. Food Secur. 1:94–98. doi:10.1016/j.gfs.2012.07.001

Van Roekel, R.J., and L.C. Purcell. 2014. Soybean biomass and nitrogen accumulation rates and radiation use efficiency in a maximum yield environment. Crop Sci. 54:1189–1196. doi:10.2135/cropsci2013.08.0546

Vega, C.R.C., F.H. Andrade, and V.O. Sadras. 2001. Reproductive partitioning and seed set efficiency in soybean, sunflower and maize. 72:163–175.

Yan, W., and I. Rajcan. 2002. Biplot analysis of test sites and trait relations of soybean in Ontario. Crop Sci. 42:11–20. doi:10.2135/cropsci2002.0011

Zhang, L., S. Kyei-Boahen, J. Zhang, M. Zhang, T. Freeland, C.E. Watson, Jr., and X. Liu. 2007. Modifications of optimum adaptation zones for soybean maturity groups in the USA. www.plantmanagementnetwork.org/cm/. Crop Manage. 6. (Bergh.). doi:10.1094/CM-2007-0927-1001-RS