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Defoliation affects soybean yield depending on time and level of light interception reduction

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Abstract

Light interception during the critical growth periods of soybean may be a suitable index for calculating the economic injury level (EIL) rather than measuring the insect population or percentage of defoliation. Our aim was to simulate the effects of time and levels of defoliation on soybean seed yield, its numerical components and light interception during the critical growth periods. We evaluated a combination of defoliation levels (0, 33, 66 and 100%) and two times of defoliation during soybean development (pod initiation and beginning of seed filling, i.e. R3 and R5, respectively). We measured the effects of radiation interception on seed yield and its components during the linear seed filling period (R5.5). The results showed that the total defoliation performed at R3 significantly reduced the seed yield compared to defoliation at R5 ($P<0.0001$) (90% and 21% yield reduction, respectively, as compared to controls). Similarly, total defoliation performed at R3 reduced seed number by 85%, whereas that performed at R5 reduced seed number only by 3%, as compared to controls ($P<0.0001$). Seed yield and its components were significantly reduced when defoliation was applied at R3, because the radiation interception at R5.5 was reduced ($P<0.001$). The photosynthetically active radiation (PAR) interception during the critical period (R5.5) was reduced only by total defoliation irrespective to the time of defoliation, evidencing the high vegetative plasticity of soybean. Our results provide a useful base for the development of economic injury levels (EILs) based on light interception during the growth critical periods.

Keywords: economic injury level, critical period, defoliating insects, seed yield, soybean ecophysiology.
Abbreviations: EIL-economic injury level; IPM- integrated pest management; LAI- leaf area index; R3-R5- seed set; R5-R7-seed filling periods; R3-pod initiation; R5- beginning seed filling; R5.5 – linear seed filling; R8 – full maturity ; I0- solar radiation at the top of the canopy; IT- solar radiation below the canopy; PAR- photosynthetically active radiation.

Introduction

The current agricultural lands in many areas of South America are predominantly cropped with soybean. South America encompasses about 44% of the world's soybean production (FAOSTAT, 2011), which provides the main incomes of countries such as Brazil, Uruguay, Bolivia, Paraguay and Argentina. The high proportion of soybean in cropped areas has led to noticeable changes in the dynamics of insect populations and their behaviour (Aragón et al., 1997). In fact, it has been noticed that the extensive areas of a crop may become the important source of feed for many insects, which may lead to a dramatic increase in their populations (Fichetti, 2007). Defoliating insects, mainly larvae of the genus Lepidoptera, family Noctuidae, are within the most important constraints for both the soybean production (Rogers and Brier, 2010 b; Timisina, 2007) and the sustainable cropping systems due to the associated increasing needs of pesticides for their control (Higley and Pedigo, 1993). These larvae consume leaf tissues and; thus, cause defoliation (Gil et al., 2003), which affects light capture and crop yields.

The concept of economic injury level (EIL) has been developed to achieve a rational and more efficient control of Lepidoptera larvae (Stern et al., 1959), in the light of an integrated pest management (IPM) (Higley and Pedigo, 1993). Economic injury level has been defined as "the lowest population density of a pest that will cause economic damage" (Stern et al., 1959). Accordingly, most EILs of many crops and their associated insects depend on the insect population (Kogan et al., 1977; Naranjo et al., 1996; Rogers and Brier, 2010a), mainly due to the practicality of insect population assessment (Higley and Pedigo, 1993).

The calculation of EIL in soybean is complex and based on bioeconomics (Haile et al., 1998), but usually includes the insect population level and the percentage of leaf defoliation (Kogan et al; 1977, Rogers and Brier, 2010a) at a given crop development stage. Although the inclusion of crop parameters is an important feature of EIL for soybean, the use of level of defoliation may be inadequate since it is estimated on the total green leaf area. Total green leaf area or vegetative biomass in soybean can be very variable depending on the sowing date (Heatherly, 1988), row spacing (Taylor, 1980; Hammond et al., 2000), plant density (Egli, 1994), genotype (Liu et al., 2005), cropping system (Caviglia et al., 2011) and availability of water (Taylor, 1980) and nutrients. The calculation of economic injury levels based on mechanistic crop parameters (such as light interception) could be more accurate than EILs, which is mainly associated with the defoliation level (Hammond et al., 2000; Ziems et al., 2006). In fact, seed yield penalties caused by insect defoliation are related to reductions in light interception

(Haile et al., 1998; Ziems et al., 2006). Light interception is directly associated with the soybean crop growth rate during the seed set (R3-R5) and seed filling periods (R5-R7) (Gardner et al., 1985), which account for most of the variation in soybean seed yields (Egli and Bruening, 2000; Calviño et al., 2003; Caviglia et al., 2011). The linear seed filling period (R5.5), i.e. when leaf area index (LAI) reaches its maximum level, is reported as the most critical stage for defoliation (Fehr et al., 1981). Although there are several reports on the effect of the reduction of light interception caused by defoliation on soybean yield parameters, the level and time of defoliation have been scarcely used to establish a threshold to evaluate yield penalties at a given phenological stage. Thus, the aims of this work were (1) to evaluate the effects of the level and time of artificial defoliation on light interception, seed yield and its components in a soybean crop, and (2) to establish the relationships between light interception during the seed set period and seed yield and its components.

Results and discussion

Environmental conditions

During the growing season (December 2006-May 2007), cumulative rainfall in the region was 50% higher than the historical value (Table 1). The soybean critical period (R4-R6) took place between March and April. During this period, the average temperature was similar to the historical value, and global radiation in the crop season was lower than the historical record for these months (Table 1).

Light interception

The light interception at R5.5 differed ($P<0.0001$) between the levels of artificial defoliation. Light interception at R5.5 differed ($P<0.0001$) between total and the remaining levels of defoliation, irrespective of the stage (R3 or R5), at which the defoliation treatments were performed (Fig. 1). It should be noted that control treatments did not reach full cover.

Seed yield per unit area

The levels of defoliation differently affected the seed yield according to the time of defoliation, in which there was a significant interaction ($P<0.0001$) between level and time of defoliation (Fig. 2). For defoliation performed at R5, the level of defoliation did not affect the seed yield (Fig. 2), whereas for defoliation performed at R3, seed yield was intermediate in plants with a low and intermediate level of defoliation (33 and 66%) and dramatically lower in plants with total defoliation, compared to control. In fact, total defoliation performed at R3 reduced seed yield by 90% ($P<0.0001$) as compared with the control. These results are in agreement with Pickle and Cavinnes (1984), who found reductions in seed yield only when high defoliation levels (75-100%) were used during late reproductive stages. Our results are in contrast with many authors (Goli et al., 1986; Board et al., 1994; Board and Harville, 1998) who reported seed yield reductions up to 40-80%, as affected by defoliation at R5. This result may be attributed to the strong source limitation under our experimental conditions driven by the low solar radiation and temperature as well as the short photoperiod which may have severely reduced the duration of seed filling period. Thus, the very restrictive source conditions of late planting dates (Calviño et al., 2003), double cropped soybean (Caviglia et al., 2011) and the reported high reproductive plasticity, which has the ability to remove the storage reserves of stems and leaves (Borrás et al., 2004), may lead to only a moderate advantage in controls as compared with defoliate treatments.

Seed and pod number per unit area

The levels of defoliation significantly affect the seed number within each time of defoliation, in which there was a significant interaction ($P<0.0001$) between level and time of defoliation (Table 2). When defoliations were performed at R3, the seed number differed between total defoliation and the remaining defoliation levels ($P<0.0001$) (Table 2). In contrast, when defoliations were carried out at R5, the seed number was not affected. There was also a significant interaction ($P<0.0001$) between level and time of defoliation for pod number per unit area (Table 2). When defoliation was performed at R3, the pod number differed between total defoliation and the remaining defoliation levels, whereas when defoliation was performed at R5, the defoliation treatments showed no significant differences ($P<0.0001$). The pod number was about 32% lower, when defoliation was performed at R3, compared to R5 (Table 2). Total defoliation performed at R3 reduced the seed number by 85%, compared to controls. The total defoliation at R5 reduced the seed number only by 3% (compared to the control) (Fig. 3a). Similarly, total defoliation performed at R3 reduced the pod number by 74% (Fig. 3b). Reduction in seed number due to defoliation was directly related to the decrease in pod number. In fact, pod number accounted for 70% of seed number variation ($P<0.0001$). This may be due to the fact that pods are being differentiated at R3, which would result in lower pod number and consequently lower seed number, which is the main seed yield component. Our results are supported by Board and Tan (1995) and Jiang and Egli (1995), who demonstrated that seed number and pod number are limited by the source photoassimilate supply during the critical period. Thus, optimizing the crop growth rate by improving light interception during the critical period is a challenge to maximize the pod and seed number.

Weight per seed

The levels of defoliation differently affected weight per seed within each time of defoliation, in which there was a significant interaction ($P<0.01$) between level and time of defoliation (Fig. 4). Defoliations performed at R5 caused minor changes in seed weight, whereas total defoliation performed at R3 decreased seed weight by 32% as compared to the control (Fig. 4). Our results are in agreement with those of Borrás et al. (2004), who found that weight per seed decreased when the availability of assimilates by effects of defoliation or shading was reduced. These authors emphasized that the decrease in weight per seed in soybean, as affected by source reduction, is important although not close to reach a 1:1 ratio, suggesting a considerable ability of the crop to mobilize reserves from vegetative tissues. The role of vegetative biomass in sustained growth under source reductions has been emphasized elsewhere (Caviglia et al., 2011). Some authors have reported weight per seed reductions by source restrictions as high as 30% as compared to control (Board et al., 1994, Goli 1986; Egli et al., 1984). However, our results are compatible with Andrade and

Table 1. Monthly means of solar radiation, temperature and rainfall during the growing season of soybean (2006/07). Monthly historical records (1934-2005 period) are shown for comparison.

		Dec	Jan	Feb	Mar	Apr	May
Solar Radiation	2006/07	22.6	22.1	20.3	13.8	11.7	10.9
MJ m^{-2}	Historical	23.7	22.9	20	17.6	13	10.4
Temperature	2006/07	24.6	24.6	24.1	21.3	19.1	13.1
ºC	Historical	23.4	24.8	23.8	21.8	18.1	15.4
Rainfall	2006/07	406.2	121.5	123.5	524.1	58.8	58
mm	Historical	117.3	117.9	104.5	152.1	106.7	49.4

Table 2. Seed and pod number per unit area at different levels and stages of defoliation. Distinct letters indicate differences between the level of defoliation within each stage of defoliation, according to Tukey's test (p≤ 0.05).

Stage of defoliation	Level of defoliation %	Seed number ±SD Number m^{-2}	Pod number±SD Number m^{-2}
Control		2329.5±128	1448.5±51
	33	2345±269a	1475±66a
R3	66	2096±174a	1281±323a
	100	384±187b	467±57b
	33	2074±157a	1304±51a
R5	66	2527±250a	1819±358a
	100	1873±536 a	1658±113a

Ferreiro (1996) who found only 3% reduction in weight per seed at R5 by shading. The weight per seed recorded in our experiment was lower than the usual values for the genotype. This may be attributed to a lower global radiation during the seed filling period (Table 1). This decrease in global radiation was related to rainfalls, which were 50% higher than normal. These meteorological conditions may have accentuated the decrease in source, typical of double-cropped soybean in our region (Caviglia et al., 2011).

Relationships between PAR interception, yield and its components

The seed yield increased significantly when the proportion of light interception at R5.5 increased. In fact, it was increased to a greater extent when defoliation was performed at R3 (R^2=0.86; P<0.0003) than when it was performed at R5 (R^2=0.55; P<0.1). The differential response of time of defoliation to PAR interception at R5.5 is due to total pod and seed number, which has already been set at R5 (Board and Tan, 1995). The reduction of PAR interception at R5.5 led to a linear reduction (R^2=0.99; P=0.0001) in weight per seed only when defoliation was performed at R3. Defoliation at R5 caused a reduction of PAR interception (16-72%) and weight per seed (4-22%) at R5.5. The weight per seed was reduced by 0.42% as PAR interception at R5.5 decreased (1%) for defoliation treatments performed at R3. In contrast, weight per seed was not significantly reduced by solar interception reduction for defoliations performed at R5.

When defoliation was performed at R3 (excluding total defoliation), seed number was reduced by 15%, although solar interception increased 8% on average (R^2=0.99; P<0.0005). Total defoliation performed at R5 reduced the seed number only by 3% as compared to the control, although solar interception was reduced by 71%. Our results support those of Borrás et al. (2004), who stated that soybean has the ability to increase weight per seed when photoassimilate is available during seed filling periods.

Relationships between seed yield and its components

Pooling all data, seed yield was more strongly associated with seed number (R^2=0.95; P<0.0001) than weight per seed (R^2=0.72; P<0.0001). This result is coincident with many studies reporting that the variation in seed yield is closely associated with the changes in the seed number and that the relationships between weight per seed and seed yield are not as important (Board and Harville, 1993; Board and Tan, 1995 and Jiang and Egli,1995; Caviglia et al., 2011). Weight per seed (R^2=0.95; P<0.0001) and seed number (R^2=0.99; P<0.0001) were significantly associated with seed yield when defoliations were performed at R3. However, when defoliations were performed at R5, seed yield was only weakly (R^2=0.66; P=0.02) related to seed number. The seed number increased significantly with the increase in the pod number, when defoliation was performed at R3 (R^2=0.99; P<0.0001). However, when defoliation was performed at R5, these variables were not significantly correlated (P>0.1). Defoliations affected the PAR interception at R5.5 and similarly when they were performed at R3 and R5 (Fig. 1). The level of PAR interception at R5.5 affected seed yield differently according to the time of defoliation (Fig. 5). For example, seed yield penalties were higher in plants defoliated at R3 than R5, on a similar level of PAR interception at R5.5. Overall, our results are useful and provide an interesting platform for the development of economic injury levels (EILs) based on mechanistic crop parameters such as light interception during the critical period. The use of EILs based on the level of defoliation should not be encouraged, since the total leaf area developed in soybean is strongly affected by the management, genotype and meteorological conditions.

Materials and methods

Study site

The Argentinean Pampas, located between 28º and 40°S and 68º and 57°W, have a warm temperate climate (Caviglia and Andrade, 2010). The mean annual temperatures increase from 13.5 ºC in the south to 18.5 °C in the north of the region (Hall et al., 1992). The mean annual rainfall increases from the southwest (SW) to the northeast (NE). The range is from 400 mm in the SW to more than 1200 mm in the NE. Soils of the Argentinean Pampas are predominantly Mollisols, with Haplustols and Argiudols as the most representative ones. The texture of soils has a gradient from sandy and sandy-loam in the SW to clay and clay-loam in the NE (INTA-SAGyP, 1990).

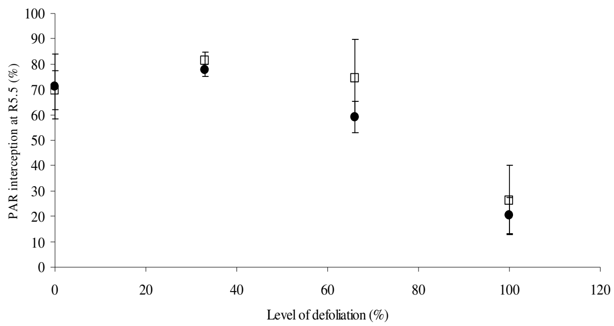

Fig 1. Interception of photosynthetically active radiation (PAR) measured at linear seed filling (R5.5) as a function of the level of artificial defoliation in soybean. Open squares ( ) indicate defoliations performed at pod initiation (R3) and closed circles (●) indicate defoliations performed at the beginning of seed filling (R5). Means of 100% defoliation differed of the other defoliation levels, according to Tukey's test (p≤0.05). There was no significant interaction between level and time of defoliation.

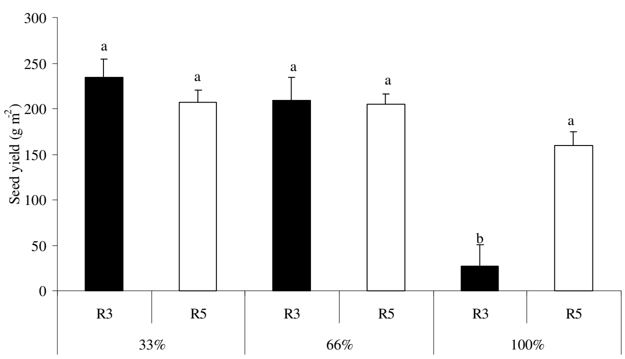

Fig 2. Seed yield at different levels and times of defoliation. Distinct letters over the columns indicate differences between stages of defoliation within each level, according to Tukey's test (p≤0.05). Black bars: defoliation performed at R3, White bars: defoliation performed at R5. Error bars indicate SD.

The experiment was conducted in the experimental station of INTA Paraná (Entre Ríos, Argentina, 31.5º S; 60.31º W; 110 meters above sea level) on a fine, mixed, thermic Aquic Argiudoll. Soybean was planted on December 21, 2007, in rows 0.53 m apart. The genotype was LAE 9972503, maturity group VI. Each plot was 1.5 m wide and 3 m long. The experimental design was a randomized complete block. Treatments resulted from the combination of three levels of defoliation (low: 33%, intermediate: 66%, and total defoliation: 100%) and two times for defoliation: R3 and R5 (Fehr and Cavinnes, 1977), i.e. pod initiation and beginning of seed filling, respectively. An additional plot, which was not defoliated, was used as control (0%). Defoliation was performed at a single opportunity, at R3 or R5, by removing one, two or three leaflets from each trifoliate leaf (Fig. 6), depending on the target level (33%, 66% and 100%, respectively).

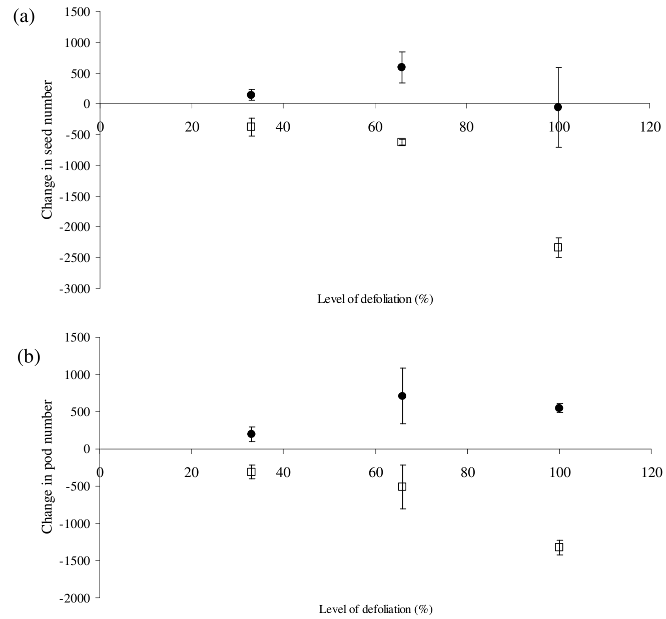

Fig 3. Changes in the average of seed number (a) or pod number (b) relative to the control at different levels of artificial defoliation in soybean. Open squares ( ) indicate defoliations performed at pod initiation (R3) and closed circles (●) indicate defoliations performed at the beginning of seed filling (R5). Error bars indicate ±SD.

Measurements

Soybean phenology was periodically recorded using Fehr and Caviness (1977). Light interception was measured at R5.5 after the last defoliation, using a linear quantum sensor (Cavadevices, Buenos Aires, Argentina). Measurements were then taken between 12:00 h and 14:00 h in full-sun conditions. In each plot, the measurements were performed at the top of the canopy (I0) and below the canopy (IT), with three replicates per plot. Light interception was calculated as:

Light interception (%) = (I0 – average IT)/I0 x 100

At R8, the shoot biomass of the central row of each plot was harvested in an area of 1 m^2. Pod number per plant and plant number were recorded and total biomass and seed yield were determined by weighing, after oven-drying for 48 h. Two sub-samples of 500 seeds were also weighed in each plot.

Calculations

We estimated seed number as the quotient between seed yield and weight per seed and harvest index as the quotient of seed yield and shoot biomass. Data were analyzed using ANOVA and Tukey's test (p≤0.05). The association between variables was evaluated using correlation analysis. Statistical analysis was performed using the procedures included in SAS (SAS, 2000).

Conclusions

Seed yield was affected only by total defoliation, mainly when it was performed at pod initiation (R3).

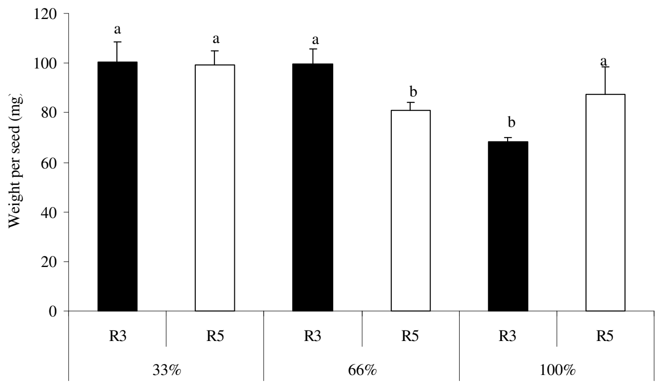

Fig 4. Weight per seed of soybean at different levels and times of defoliation. Distinct letters over the columns indicate differences between the time of defoliation within each level of defoliation, according to Tukey's test (p≤ 0.05). Black bars: defoliation performed at R3, White bars: defoliation performed at R5. Error bars indicate ±SD.

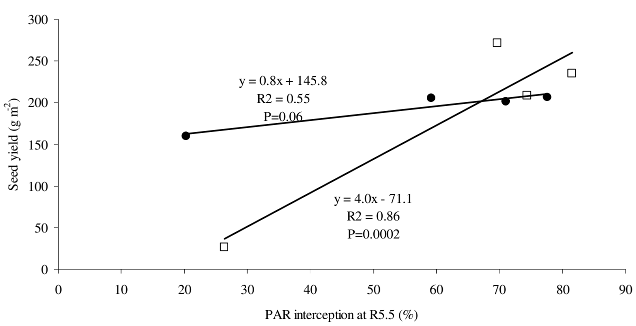

Fig 5. Seed yield as a function of PAR interception at linear seed filling (R5.5). Open squares ( ) indicate defoliations performed at pod initiation (R3) and closed circles (●) indicate defoliations performed at the beginning of seed filling (R5). Error bars indicate ±SD.

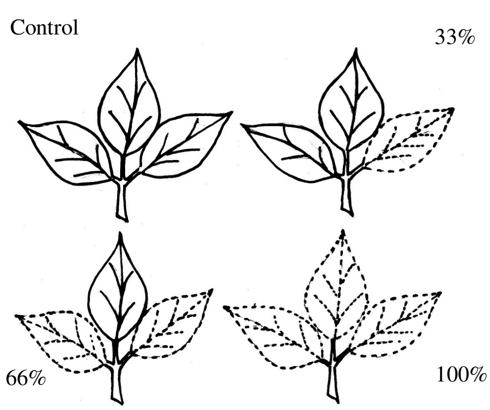

Fig 6. Schematic representation of the levels of artificial defoliation performed at R3 and R5 in the soybean. The desired level was reached by removing one, two or three leaflets of each leaf.

Total defoliations performed at this stage affected seed number to a larger extent than weight per seed. Irrespective of the time of defoliation, PAR interception during the critical period (R5.5) was reduced only by total defoliation, evidencing the high vegetative plasticity of soybean. In fact, soybean leaf area may recover after defoliation since its expansion continues through flowering and fruiting, even in genotypes with determinate growth habit and late planting date. The level of PAR interception at R5.5 affected seed yield differently according to the time of defoliation. At a similar level of PAR interception at R5.5, seed yield penalties were higher in plants defoliated at R3 than in those defoliated at R5.

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