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Post-flowering leaflet removals increase pod initiation in soybean canopies

Alvaro Quijano, Eligio N. Morandi*

Cátedra de Fisiología Vegetal, Facultad de Ciencias Agrarias, Universidad Nacional de Rosario. Campo Experimental J. Villarino s/n. PO Box 14, 2125 Zavalla, Santa Fe, Argentina

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ABSTRACT

Much of the yield variation in soybean (*Glycine max* L. Merrill) crops is related to changes in pod and seed number. Pod number is the result of pod initiation and pod abscission while seed number is the result of potential seed per pod and seed abortion. However, the physiological regulation of these processes is not well understood. A field experiment was conducted to investigate the role of post-flowering changes in source size and canopy structure on pod initiation, pod abscission and seed abortion in soybean. Two soybean genotypes: DM48 and A7409 (maturity groups IV and VII, respectively) were used. Leaflet removal treatments (L) consisted of removing none (L0), one (L1) or two (L2) lateral leaflets of every developed trifoliate leaf present. Leaflet removals were applied twice: the first at full bloom and the second shortly after the beginning seed stage. Crop growth rate (CGR), leaf area index (LAI), light interception (LI), and relative leaf growth rate, were determined during the periods in which numerical components are established. For the period between the first and the second leaflet removal, CGR remained unchanged among L treatments in both genotypes because LAI reductions were compensated through an increase in the net assimilation rate of the remaining leaves. The first leaflet removal increased the relative leaf growth rate and the number of pods initiated (PI) and these increases were inversely related to the remaining LAI in both genotypes. Moreover, the inverse relationship between LAI and PI was sustained at LAI below and above critical (i.e., LAI for 95% LI) and was not related to CGR or LI. The number of pod abscised also increased with the level of leaflet removal during the first and main abscission period in both genotypes and the percentage of pod abscission was directly related to the seed growth rate per unit leaf area during the abscission period. Seed abortion was inversely related to LAI after the second leaflet removal. Only the highest level of leaflet removals (i.e., L2) was able to reduce seed size in both genotypes. Whereas pod abscission, seed abortion and seed size could be related to indicators of canopy assimilatory capability pod initiation was not, suggesting that other physiological mechanism/s operate in the regulation of pod initiation. In addition, our results suggest that early (i.e., at flowering) canopy closure may negatively impact pod initiation in soybean. To the best of our knowledge, this study is the first to document that the number of initiated pods is inversely related to LAI in soybean canopies.

1. Introduction

The primary components of soybean yield are seed number (seed/m^2) and seed size (mg/seed). Improvements in agronomic practices or genetic gains could increase future yields by increasing seed number, seed size, or both components. Pod number has been shown to be highly associated with seed number because the actual number of seeds per pod shows low environmental variation (Egli, 1998). Assimilate availability has been considered to be the main factor that regulates pod and seed number changes (Board and Tan, 1995; Jiang and Egli, 1993). Variations in leaf area index (LAI), light interception (LI), or crop growth rate (CGR), which is an index usually used as an estimator of canopy photosynthesis, have been associated with differences in pod and seed number (Herbert and Litchfield, 1984; Ramseur et al., 1985; Board and Harville, 1994; Board and Tan, 1995). Linear relationships between LI or CGR measured from full flowering to the beginning of seed growth, and pod or seed number at maturity were then considered as evidence that pod and seed number are source-limited (Egli and Zhen-wen, 1991; Board et al., 1995; Board and Harville, 1998). These models explain well the relationship between pod or seed number and CGR when CGR is abruptly reduced through defoliation or shading, but the association becomes weak when additional genetic or environmental factors are involved (Egli and Bruening, 2000). On the other hand, there are situations where CGR increases significantly while seed number remains unchanged, which indicate that higher CGR does not necessarily mean higher

* Corresponding author at: Cátedra de Fisiología Vegetal, Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, Campo Experimental J. Villarino, PO Box 14 (S 2125 ZAA), Zavalla, Santa Fe, Argentina.
Tel.: +54 341 4970080; fax: +54 341 4970085.
E-mail address: emorandi@unr.edu.ar (E.N. Morandi).

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partition of assimilates to reproductive structures (Quijano et al., 1998).

Pod number is determined by pod initiation and pod abscission, and seed number is determined by the potential number of seeds per pod and seed abortion. These components are sequentially established and partially overlap during development. They may also have different physiological and/or environmental requirements for reaching their maximum potentials. In addition to assimilates, other environmental and/or internal signals may affect soybean pod initiation and abscission (Heindl and Brun, 1983; Myers et al., 1987; Kokubun and Honda, 2000) as well as seed number and filling (Morandi et al., 1988, 1990).

In this study we investigated the effects of changes in post-flowering source size and canopy structure on pod initiation, pod abscission, and seed abortion in soybean. Evidence will be presented showing that the number of pods initiated was inversely related to LAI while it was not related to CGR or LI, suggesting that other physiological mechanisms, not directly related to assimilatory capability, were involved in the regulation of pod initiation in soybean canopies.

2. Materials and methods

A field experiment was conducted at the research field of the Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, Zavalla, Argentina (33°01′ S, 60°52′ W) during the 2001–2002 growing season. The emergence date was December 1st, 2001. Soybean genotypes were DM48 (Maturity Group (MG) IV) and A7409 (MG VII), both of which had an indeterminate growth habit. These genotypes were commercial varieties that have been extensively sown in Argentina. Genotypes were over-seeded and thinned to a final seed density of 32 and 26 plants/m^2 for DM48 and A7409, respectively. Individual plots were 6 m long and 3.2 m wide (eight rows with 0.40 m between rows). The plots were irrigated when necessary to avoid water deficits. Pests, diseases and weeds were permanently controlled during the experiment. Phenological stages were defined according to Fehr and Caviness (1977). Full bloom (R2), beginning seed (R5), beginning maturity (R7), and full maturity (R8) occurred at 42, 66, 121 and 130 days after emergence (DAE), respectively, for DM48 and at 66, 87, 128 and 140 DAE, respectively, for A7409. Leaflet removal treatments consisted of removing none (L0), one (L1) or two (L2) lateral leaflets of every trifoliate leaf at R2 and again shortly after R5. Thus, the canopy structure was modified by homogeneous removal of leaflets of all developed leaves that were present at the time of treatment. The LAI was estimated using regression functions that related leaf weight with LAI data from another experiment conducted in the same field, which used the same genotypes and leaflet removal treatments. Coefficients of determination (R^2) for these functions ranged from 86% to 99% and were statistically significant in all cases ($P < 0.05$).

A radiation sensor (pyranometer), an air temperature sensor and a bucket rain gauge were connected to a LI-COR LI-1200 Data set recorder to measure incident global solar radiation, temperature and rainfall. Sensor instruments were placed near the experimental plots. Statistical differences between climatic variables were determined by *t*-tests using standard errors.

The experimental design was a split plot with three replicates. Genotypes (G) were the main plots, and they were arranged in a randomised, complete block design. Leaflet removal treatments were randomised within each main plot and applied two times (T1 and T2). For DM48, leaflet removals were performed at phenological stages R2 (T1) and R5 + 7 d (T2), which were 42 and 73 DAE, respectively. For A7409, leaflet removals were performed at R2 + 4 d (T1) and R5 + 13 d (T2), which were 70 and 100 DAE, respectively. The period from T1 to T2 was named Per1, and the period from T2 to R7 was named Per2.

Light interception (photosynthetic active radiation, PAR) was measured immediately after T1 and T2 with a LI-COR Line Quantum sensor (LI-COR, Lincoln, NE) connected to an LI-1000 data logger. Percentage of light interception was determined in each plot from readings made above the canopy and at ground level. Measurements were taken on clear day, between 1130 and 1400 h solar time. Line quantum was placed on the ground diagonally between the plot rows. In each plot, two readings were taken at different random positions. The LI values on the other dates were estimated by a function developed from the relationship between LI and LAI for DM48 ($R^2 = 0.97$, $P < 0.0001$) and A7409 ($R^2 = 0.95$, $P < 0.0001$).

The extinction coefficient of the canopy (k) was obtained from the Lambert-Beer's law, such that, $k = -\ln(I_i/I_0)/\text{LAI}$, where ln means natural logarithm, I_i is PAR at soil level and I_0 is PAR above the canopy (Gardner et al., 1985).

Between T1 and T2, four destructive samples of 0.25 m^2 were taken for both genotypes. Between T2 and R7, three destructive samples were taken for DM48, and two destructive samples were taken for A7409. For each sample, all plants were separated into stems, leaves (petioles plus leaflets), pods and seeds (when present). Samples were dried to a constant weight at 60 °C in a forced-air dryer, and dry matter was expressed as grams per square meter (land basis).

The number of pods was counted in all sampled plants at 54, 72, 83, 97 and 111 DAE for DM48 and at 81, 87, 94, 103 and 115 DAE for A7409. A pod was counted when it was visible (≥2 mm). The number of pods initiated (PI) was defined as the maximum number of pods in the flush minus the minimum number of pods before the flush. The number of pods abscised (PA) was defined as the maximum number of pods in the flush minus the minimum number of pods after the flush.

Total dry matter (TDM) per land area during the R5 to R7 period was increased to account for the photosynthate requirement of seed production [2 g of photosynthate required to produce 1 g of seed dry weight (Sinclair and de Wit, 1975)]. Total dry matter and LAI were regressed against time (Hunt and Parsons, 1981) to obtain the following indices: CGR [g/m^2 (land area)/d], NAR [net assimilation rate, g/m^2 (leaf area)/d] and relative leaf growth rate [m^2/m^2 (leaf area)/d]. Linear, quadratic and cubic components of each regression equation were successively tested for significance and included in the equation if they significantly reduced the residual sum of squares. Significant differences were determined by *t*-tests using standard errors calculated by the regression program. Seed growth rate (SGR) was calculated as the slope of the regression function of increased seed dry matter over time during the linear seed-growth period. The date of initiation of linear seed growth was estimated by dividing the origin ordinate of the regression function by SGR.

At maturity, a 1-m^2 area was harvested by cutting the plants at ground level. Harvested plants were separated into main stems, branches, seeds and pod walls. Seed size (mg/seed) was calculated as the mean dry weight of 480 randomly sampled seeds. Maturity seed number (seed/m^2) was calculated as seed yield (g/m^2) divided by seed size. Maturity pod number (pod/m^2) was calculated as the final seed number divided by the actual seeds per pod at maturity.

A sample of 10 plants was used to determine the branch number, the main stem and branch node number and the number of pods in the main stem and branches. The potential seed number per pod was established by counting the number of pods with 2 (loc2), 3 (loc3) and 4 (loc4) loculi and then resolving the following equation: [(loc2 × 2) + (loc3 × 3) + (loc4 × 4)/total pod number]. A loculus was counted if a remnant of seed structure was visible in a partially or fully developed pod loculus. Potential seed number was determined by the potential seed number per pod multiplied by the pod number at maturity. Seed abortion was calculated as the actual seed number divided by the potential seed number. The