Source-sink relationship of soybean accessed by increasing in solar radiation through the plant canopy

Samuel Luiz Fioreze[1*], Walter José Heck Gotz[1], Thais Lemos Turek[2], Ana Carolina da Costa Lara Fioreze[1]

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ABSTRACT

The photosynthetic metabolism is a key point to improve soybean yield. In this work, we demonstrated that radiation use by soybean plants can be improved, aiming to improve the grain yield in the lower canopy. The objective of this study was to observe whether the increase in solar radiation input in the canopy of soybean plants improves their yield performance. Three experiments were carried out during the 2017/2018 season. For each experiment, treatments consisted in the opening of one or two side rows of cultivation at the R2 and R5 stage of soybean plants (NA5909RR) until maturity, plus a control. Increase on solar radiation provided by the oppening of rows enhanced the yield potential in the nodes of the lower canopy, mainly when two rows were opened. The main benefits of increasing the radiation available throughout the canopy of soybean plants are observed in the number of pods and thousand-grain weight, demonstrating the importance of increasing the availability of assimilates in lower leaves. Interestingly, the benefits of the increase in solar interception were observed regardless of the yield potential of the area, which varied between 4.9 and 6.7 ton ha^{-1}.

Keywords: *Glycine max* L. Merril; photosynthesis; yield improvement.

INTRODUCTION

Soybean is the world's leading commodity due to its unquestionable importance to human health and diet. Currently, the global production of soybean is 361.1 million tons (USDA, 2019), so the constant increase in its consumption stimulates research that seeks to increase the productive efficiency of the crop. Considering that photosynthesis is a key process for crop yield, studies on the factors involved with carbohydrate metabolism have been increasingly frequent and one of the main focuses has been the relationships between the source and sink of the crop (Ainsworth *et al.*, 2012; Koester *et al.*, 2014).

Historically, research has shown that soybean crop has a high level of variation in responses to source-sink modifications, evidencing a characteristic of co-limitation, which is variable according to genotype and study conditions (Borrás *et al.*, 2004). Bernacchi *et al.* (2006) suggested that soybean yield is limited by the strength of sinks, since the increments in production are significantly lower than those observed in the CO_2 assimilation rate (*A*). However, much attention has been given to the study on the increase in the efficiency of carbon metabolism in single leaves of the upper canopy of soybean plants or even to studies conducted in a protected environment. Van Loon *et al.* (2014) demonstrated the importance of considering competition between plants in order to obtain accurate data on the responses of soybean plants to a certain environmental condition. Additionally, the ratio between leaves within the canopy of plants should not be overlooked.

Many studies published in the field of the study on source-sink relationships have addressed environmental stress (drought or shade) or the physical manipulation of the relationship between leaves and pods as study tools (Kokubun *et al.*, 2001; Liu *et al.*, 2004a; Egli & Bruening, 2005). Although they are of great importance for studying

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[1] Universidade Federal de Santa Catarina, Departamento de Ciências Biológicas e Agronômicas, Curitibanos, Santa Catarina, Brazil. s.fioreze@ufsc.br; heckgotz@gmail.com; ana.lara@ufsc.br
[2] Universidade do Estado de Santa Catarina, Centro de Ciências Agroveterinárias, Fisiologia e Manejo de Plantas de Lavoura, Lages, Santa Catarina, Brazil. thaisturek@yahoo.com.br
Corresponding author: s.fioreze@ufsc.br

carbohydrate metabolism in the plant, the imposition of stress via limitation of sources or through the physical manipulation of sinks promotes pleiotropic effects on plants, which can often mask plant responses. In this context, little has been studied about the simulation of the increase in radiation input in the lower third of plants, which has a low participation in the total grain yield of the plant due to the lower interception of solar radiation (Schwerz *et al.*, 2019). Considering those, it is possible to improve photosynthetic activity and pod set in this portion of plants, as demonstrated by Schou (1978).

Considering the high efficiency values of radiation interception (**ε**i) observed in soybean crop (90%) (Ainsworth *et al.*, 2012), a strategy to increase yield could be associated with increment in the conversion of incident radiation into biomass (**ε**c) (Monteith, 1977) and also increase in the harvest index (**ε**p) referred to as the efficiency with which biomass is partitioned in grain production (Zhu *et al.*, 2010). Although the increase in the grain filling period may be an important feature, this could result in increased costs with management of pests and diseases of the crop. Thus, increasing the conversion of incident energy into biomass becomes a challenge, so that changes in leaf metabolism (photosynthesis, respiration and photorespiration), reproductive efficiency, sink strength and even nitrogen metabolism efficiency are among the main targets (Ainsworth *et al.*, 2012).

Although there are advances in the harvest index or even in the efficiency in radiation interception (Koester *et al.*, 2014; 2016), the participation of lower canopy leaves has been neglected in field studies involving this crop. Therefore, the objective of this study was to observe whether the increase in solar radiation input in the canopy of soybean plants improves their yield performance.

MATERIAL AND METHODS

Three experiments were carried out under field conditions during the 2017/2018 season, in the southern region of Brazil. The experimental area is located at coordinates 27º16’26.55" South latitude and 50º30’14.11" West longitude, with an average altitude of 987 meters. According to the Köppen-Geiger classification, the climate of the region is cfb type, with an average temperature between 15 °C and 25 °C and average annual rainfall of 1500 mm (Climate-Data, 2020). The experimental soil is classified as *Cambissolo Háplico* (Inceptisol) of clayey texture (Santos *et al.*, 2018). Its physical and chemical characteristics, as well as the main climatic variables in the period, are presented in Table 1.

The experiments were conducted in a randomized block design with five treatments and four replicates. Treatments consisted in the opening of one or two side rows of cultivation at the R2 stage and at the R5 stage of plant development (Fehr & Caviness, 1977), plus a control. Each plot was composed of three soybean cultivation rows, spaced apart by 0.40 m, with length of 1 m. The central row was considered as usable plot. The rows were opened using stakes and wires, by tilting the side rows of the usable plot to an angle of 45º (Figure 1). The objective of just tilting the cultivation rows was to interfere as little as possible in the competition for water and nutrients compared to the side rows. The rows remained open until the end of the crop cycle.

The three areas showed different conditions of cultivation. The first and second experiments were cultivated in soils with fertility between medium and high (Table 1). Experiment 1 was sown on November 3, while experiment 2 was sown on December 7, 2018. The third experiment was cultivated in low-fertility soil, in an area of first soybean cultivation, with sowing carried out on November 7, 2018. The soybean cultivar used in all experiments was NA 5909RR, which has indeterminate growth habit and relative maturity group of 6.3.

The three experiments were conducted in a no-tillage system on black oat straw. Basal fertilization for the three areas was performed with 300 kg ha^{-1} of the formulated fertilizer 02-20-20 (NPK). Seeds were treated with Imidacloprid + Thiodicarb (0.5 L 100 kg^{-1}) and Carbendazim + Thiram (0.2 L 100 kg^{-1}) and inoculated with *Bradyrhizobium japonicum*, SEMIA 5079 and SEMIA 5080 (100 g 100 kg^{-1}), immediately before sowing. At the development stage VE (Fehr & Caviness, 1977), the plant density was adjusted to 350,000 plants ha^{-1} by means of thinning.

At the end of the crop cycle, plant height and first pod height were determined. To determine the yield components, plants of the usable plot were divided into upper and lower portions. The number of pods, number of grains per plant, number of grains per pod, grain weight per plant and thousand-grain weight were determined in each portion. Yield was determined after threshing all the plants of the plot, adjusting grain moisture content to 13%.

In order to assist in the discussion of the results obtained, in the 2019/2020 season, the atmospheric concentration of CO_2 through the plant canopy was studied. The study was carried out in an area of soybean, cultivar BMX Lança RR, at R3 stage (Fehr & Caviness, 1977). Samples were collected in the lower third of the plants (0.2 m height from the soil level), in the middle third and immediately above the last leaves of the upper canopy of the plants. The measurements were performed between 10h00 and 11h00, in area where the crop was sowing on straw of wheat. The evaluations were performed with a portable gas exchange meter, Li-6400xt model, with open flow system (LI-COR® - Lincoln. Nebraska USA). The device’s air inlet was connected to a 6-m-long hose in order to increase the accuracy of the measurements.

The data were subjected to analysis of variance by the F test ($p < 0.05$). Based on the criterion of homogeneity of the mean squares of residuals between the three experiments, a joint analysis of the data was performed. The means were compared by Tukey test ($p < 0.05$) using the program SISVAR (Ferreira, 2011).

RESULTS

There were significant differences in soybean grain yield between the three cultivation areas (Table 2). The highest value of grain yield was obtained in the Expt.1 area, intermediate yield values were obtained in the Expt.2 area, while the lowest values were observed in the Expt.3 area. Such difference was already expected, because of the delayed sowing in Expt.2 compared to Expt.1 and also due to the lower level of soil fertility in Expt.3 compared to the others. Higher grain yield in Expt.1 is explained by the higher TGW, although the number of grains was lower than in Expt.2 (Table 3). Although the highest values of TGW were obtained in Expt.3, the very low values of number of grains per plant explain the lower yields obtained in this area.

The choice of the three areas allowed the occurrence of soybean plants with distinct growth patterns. Plants in Expt.1 showed higher height compared to the others. Regarding harvest height, the highest values were observed in Expt.3, which also generated plants of lower height.

The opening of two cultivation rows promoted the highest values of soybean yield, regardless of the area of cultivation, especially when applied at the R2 development stage (Table 2). Intermediate values of yield were obtained with the opening of one cultivation row, while the lowest values were observed in control plants. The increase in radiation input in the canopy of soybean plants caused a slight reduction in plant height, especially when applied at R2. This result may have arisen from the lower elongation of the last internodes of the stem apex under conditions of higher available radiation. Additionally, all treatments subjected to radiation input in the canopy caused reduction in the harvest height of

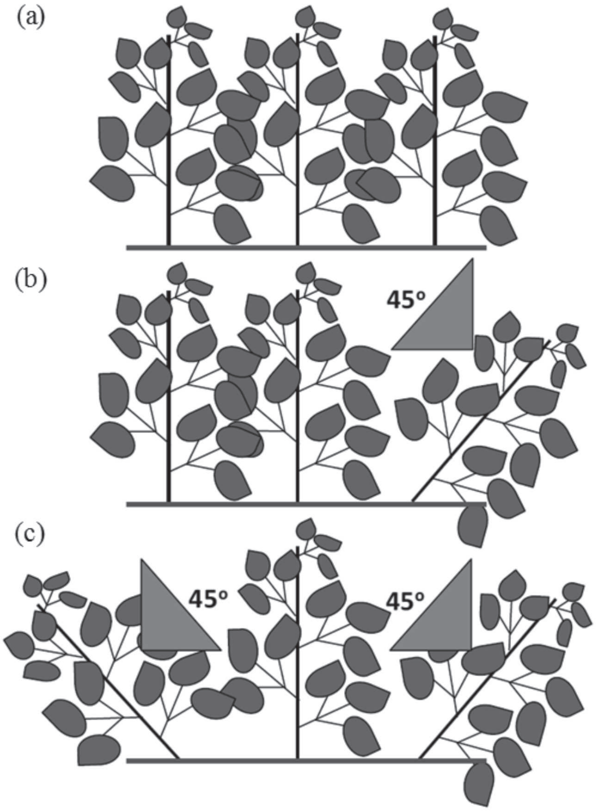

Figure 1: Soybean plant illustration for control treatment (a) and opening of one (b) or two (c) side rows of cultivation.

Table 1: Chemical characterization of the soil at 0.0-0.2 m layer, sowing dates and climatic parameters during growing season

	Expt. 1	Expt. 2	Expt. 3
pH	6.7	6.7	4.7
Ca (cmol dm^{-3})	13.3	13.3	2.6
Mg (cmol dm^{-3})	5.2	5.2	1.8
K (cmol dm^{-3})	0.2	0.2	0.5
SB (cmol dm^{-3})	18.7	18.7	4.9
Al (cmol dm^{-3})	0.0	0.0	2.5
H+Al (cmol dm^{-3})	1.8	1.8	15.4
m (%)	0.0	0.0	35.0
V (%)	91.0	91.0	24.3
OM (%)	3.3	3.3	4.3
P (mg dm^{-3})	13.1	13.1	2.0
Sowing date	Nov-03	Dec-07	Nov-07
Rainfall (mm)	906.2	765.6	876.2
Average temperature (ºC)	18.6	18.9	18.5
Total radiation (MJ m^2)	2101	1430	2054

[1]pH measured in a solution of 0.01M $CaCl_2$; V = Base saturation; m = Aluminum saturation; OM= Organic matter; [2]Mehlich-1.

the plants (Table 2). This is probably due to the greater setting of pods in nodes of the lower third of the plants, as a response to the increase in the amount of carbohydrates available in this canopy stratum.

The effects of the increment in yield (Table 2) caused by the greater input of solar radiation in soybean canopy were observed in terms of number and individual mass of grains (Table 3). The opening of rows increased the number of pods and number of grains in the lower portion of soybean plants, especially when the two side rows were opened at R2. A determining factor for the setting of soybean reproductive structures is the availability of carbohydrates (Egli & Bruening, 2001; 2002; 2005). Thus, the increment in radiation input seems to have increased the photosynthetic activity of the lower portion of the plant canopy, improving the availability of assimilates to reproductive structures.

It is interesting to note that the increase in the number of pods and grains of the lower stratum of the plants occurred even when the rows were opened at R5, when there is virtually no more pod setting (Table 3). This effect may have occurred due to the reduction of pod abortion in the lower portion of the canopy. Although the applied treatments increased the number of pods and grains, the average number of grains per pod was not affected.

Although the opening of the cultivation rows increased the yield potential of the lower portion of the plants (number of pods and grains), this effect was not observed in the upper portion of the plants considering the adopted level of significance ($p < 0.05$, Table 3). The upper stratum of the canopy naturally has greater access to available radiation.

The TGW of the lower portion of the plants was higher when the two lateral rows of the plot were opened, both at R2 and at R5 (Table 3). In this portion of the plant, the opening of only one of the side rows did not affect the TGW. On the other hand, the opening of one or two cultivation rows led to increase in the TGW of the upper portion of the plants, at both stages tested.

The higher value of grain yield in plants where the two side rows of the plot were opened at R2 is probably due to a double effect promoted by the increase in radiation input (Table 2). The first effect is the increase in the number of pods and grains and the other is the increment in grain filling, measured through the TGW, considering that the rows remained open until the end of the crop cycle.

DISCUSSION

Conducting this study in three areas allowed the occurrence of three levels of yield potential for the same soybean cultivar (Table 2). Based on this aspect, it is important to highlight that the positive effects of the increase in solar radiation input in soybean canopy result from the initial yield potential of the plants, since there was no significant interaction between the two study factors. In general, the best results obtained for the opening of rows at the R2 stage of plant development may have been caused by the time of exposure to this condition compared to the opening performed at the R5 stage.

The availability of assimilates is a primordial factor for pod setting in soybean crop (Kokubun *et al.*, 2001; Egli and Bruening, 2001; 2002; Liu *et al.*, 2004a; 2004b), as well as its interaction with hormonal balance (Yashima *et al.*, 2005). The large use of assimilates by pods in fast initial growth, from early fertilized flowers, is a determining factor for the abortion of late-produced flowers (Egli & Bruening, 2002), as it increases their potential for competition for often limited sources. This result clearly illustrates the

Table 2: Grain yield, harvest height and plant height of soybean plants (NA 5909RR) as affected by increasing on solar radiation on plant canopy at R2 and R5 stages

	Yield (kg ha^{-1})	Harvest height (cm)	Plant height (cm)
Expt. 1	6671.7 a	28.76 b	119.31 a
Expt. 2	5571.8 b	28.00 b	109.95 b
Expt. 3	4938.4 c	31.54 a	88.58 c
p	*0.00*	*0.01*	*0.00*
Control	5186.1 c	34.65 a	109.10 a
1 row at R2	5535.8 bc	27.83 b	104.40 ab
1 row at R5	5269.9 bc	29.75 b	104.98 ab
2 rows at R2	6473.8 a	26.03 b	102.50 b
2 rows at R5	6171.3 ab	28.90 b	108.75 ab
p	*0.00*	*0.00*	*0.02*
E x T (*p*)	*0.12*	*0.30*	*0.69*
CV (%)	13.59	11.79	5.13

p: probability of F test; E: experiment; T: treatment. CV: coefficient of variation; Means followed by the same letter do not differ by the Tukey test ($p < 0.05$).

competition between sinks for limited sources in a condition of field cultivation. Thus, the results obtained in the present study make it possible to point out that the improvement in the access to radiation for leaves of the lower portion of plants increased their photosynthetic activity and, therefore, the availability of carbohydrates for reproductive structures of this portion, increasing the number of pods and grains. This result reveals the importance of leaves of the lower canopy of soybean plants for composing their yield.

Despite the deleterious effects caused by the limitation to sources, using shading, the removal of 90% of soybean pods under field conditions resulted in increased sucrose content in the cotyledon of seeds in formation, increasing their individual mass (Egli & Bruening, 2001). One limitation in these results may be associated with the fact that a 90% reduction in the number of already established sinks can severely affect carbohydrate metabolism, which can mask some adaptation responses of plants. In this context, source-sink relationships could be better understood by studying variations over time and of smaller amplitude, without causing stress to plants during a highly sensitive period like the reproductive stage, mainly at flowering and pod formation stage.

Another interesting aspect to be highlighted is that studies in which the limitation in the sources of photoassimilates is imposed through shading create a condition of increase in the natural shading that occurs on leaves of the lower canopy of plants. The results observed by Fan *et al.* (2018) reveal that soybean plants have the ability to regulate characteristics of leaf morphology and anatomy according to radiation availability. Fioreze *et al.* (2013) observed that the drastic reduction in the carbon assimilation of leaves of the apex of soybean plants subjected to 80% restriction in total incident radiation was slowly overcome after 12 days, when the plants reached values of assimilation close to those of plants under full sun, indicating an adaptive mechanism. Carbon assimilation in leaves of the lower canopy of these plants, however, was not measured.

Schou *et al.* (1978) observed that the opening of soybean rows at an angle of 45º during the end of flowering

Table 3: Number of pods (NP) and number of grains (NG) per plant, number of grains per pod (NGP), grain weight per plant and thousand grain weight (TGW) of soybean plants (NA 5909RR) as affected by increasing on solar radiation on plant canopy at R2 and R5 stages

	NP	NG	NGP	GW (g)	TGW (g)
		Lower portion of the plant			
Expt. 1	13.92 b	28.64 b	2.06 b	4.34 a	151.59 b
Expt. 2	17.00 a	33.19 a	1.95 c	3.75 b	112.04 c
Expt. 3	6.31 c	13.59 c	2.16 a	2.18 c	159.71 a
p	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*
Control	10.25 c	20.58 c	2.02	2.70 c	135.45 b
1 row at R2	12.11 abc	24.46 bc	2.07	3.25 bc	136.17 b
1 rows at R5	11.17 bc	22.84 bc	2.08	3.03 c	139.86 b
2 rows at R2	14.82 a	30.33 a	2.08	4.14 a	142.90 ab
2 rows at R5	13.70 ab	27.49 ab	2.04	4.00 ab	151.20 a
p	*0.01*	*0.01*	*0.35*	*0.00*	*0.00*
AxT (*p*)	*0.07*	*0.07*	*0.91*	*0.00*	*0.12*
CV (%)	19.94	19.65	4.05	20.28	5.92
		Upper portion of the plant			
Expt. 1	39.95 b	92.53 a	2.32 b	14.72 a	158.79 b
Expt. 2	46.14 a	97.25 a	2.11 c	12.17 b	125.29 c
Expt. 3	28.50 c	68.76 b	2.41 a	11.93 b	173.26 a
p	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*
Control	36.70	82.85	2.28	12.12 b	148.00 b
1 row at R2	37.40	84.35	2.27	12.57 ab	150.59 ab
1 row at R5	35.97	81.42	2.28	12.03 b	150.32 ab
2 rows at R2	41.07	93.46	2.30	14.36 a	156.82 a
2 rows at R5	39.83	88.82	2.26	13.63 ab	156.49 a
p	*0.08*	*0.10*	*0.78*	*0.02*	*0.01*
AxT (*p*)	*0.31*	*0.37*	*0.70*	*0.22*	*0.07*
CV (%)	12.85	13.50	4.04	14.09	4.18

p: probability of F test; E: experiment; T: treatment. CV: coefficient of variation; Means followed by the same letter do not differ by the Tukey test ($p < 0.05$).

and beginning of pod formation led to increments in pod setting and, consequently, in grain yield, using or not reflective aluminum plates. In this context, it is interesting to highlight that the positive responses to this type of environment remained in a cultivar released almost 40 years after the publication of this work. The results obtained in the present study demonstrate a clear effect of the increase in the efficiency of radiation use by plants, since greater access to radiation in leaves of the lower portion maintains the "sun leaves" characteristic and can reduce losses by photorespiration. The absence of significant variations in CO_2 concentration between the upper and lower canopy of soybean plants (Figure 2) demonstrates that CO_2 is not a limiting factor for the photosynthesis of these leaves.

Although the CO_2 concentration is not a limiting factor for the lower canopy of soybean plants (Figure 2) Pieruschka *et al.* (2010) observed that soybean leaves with heterobaric anatomy do not have lateral diffusion of gases between sunny and non-sunny portions, unlike leaves of *Vicia faba*, which are homobaric. This can further reduce the performance of leaves of the lower third of soybean plants, which are in an environment with great variation of access to radiation. Thus, it is evident that the greatest limitation to the photosynthetic metabolism of leaves of the lower canopy of soybean plants is the low incidence of photosynthetically active radiation. Despite the high efficiency in the interception of incident solar radiation (εi=0.9), observed in current varieties of the USA, only 60% of the incident energy is converted into grain production (εp=0.6) (Zhu *et al.*, 2010). Based on this, the results of the present study demonstrate that the better utilization of the available radiation by the entire canopy of plants, including the leaves of the lower canopy, can increase the efficiency of conversion of energy into grain production. Similar results were obtained by Schwerz *et al.* (2019).

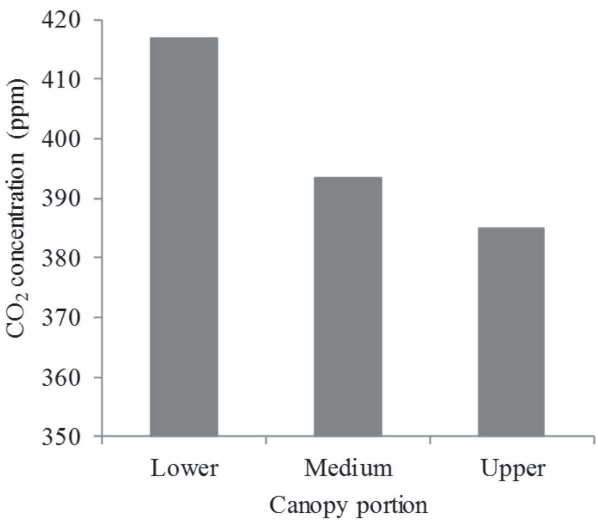

Figure 2: CO_2 concentration through soybean (BMX Lança RR) canopy between 10h00 and 11h00 at R3 stage (Fehr & Caviness, 1977).

Walker *et al.* (2018) suggested that chlorophyll content could be reduced in soybean leaves without compromising photosynthesis. However, the authors did not consider the restrictions on the access to radiation in the lower canopy of plants, since single rows were used in the study. According to Slattery *et al.* (2016), reduction in the amount of chlorophyll b (investment in antenna complex) could improve the distribution of available radiation between chloroplasts through leaf cell layers, although the results are not absolutely conclusive. In this case, the reduction of chlorophyll b content would not necessarily imply a reduction in the total content of photosynthetic pigments, but a possible change in the proportion between antennae and reaction centers along the canopy of plants. Studies conducted with recent soybean cultivars show that higher daily rates of carbon assimilation occur under conditions of high stomatal conductance and good water content available in the soil, in addition to high chlorophyll content and higher sink strength in the final portion of grain filling (Koester *et al.*, 2016).

It is important to highlight that the results presented by Koester *et al.* (2014; 2016) were obtained under cultivation conditions of the USA, which has higher latitude of cultivation and, consequently, longer daily duration of the radiation period available during grain filling. In addition, the authors used spacing of 0.76 m between cultivation rows, in contrast to the values between 0.40 and 0.50 m practiced in Brazil. Van Loon *et al.* (2014) demonstrated the importance of considering the competition between plants to obtain more accurate data of soybean responses to a given environmental condition.

The results observed in the present study demonstrate that soybean plants may present increased production under conditions where the capacity of the sources is increased overall. Thus, even with the development of modern cultivars, such as the one used in the present study, there is still much to be improved in relation to the access of the lower canopy of plants to photosynthetically active radiation. These improvements will certainly be associated with changes in the architecture, orientation or even size of leaflets, as well as changes in the ultrastructure of chloroplasts and also in the photosynthetic metabolism of plants.

CONCLUSIONS

Increase in radiation input in soybean canopy can increase the yield potential of plants, especially in the nodes of the lower canopy.

The main benefits of increasing the radiation available throughout the canopy of soybean plants are observed in the number of pods and thousand-grain weight.

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