Acta Scientiarum

http://www.periodicos.uem.br/ojs/
ISSN on-line: 1807-8621
Doi: 10.4025/ actasciagron.v44i1.55639

CROP PRODUCTION

Soybean tolerance to defoliation at the vegetative and reproductive stages as a function of water restriction

Lucieli Santini Leolato*, Luís Sangoi, Clovis Arruda Souza, Hugo François Kuneski, Rafael Leandro Scherer, Vander de Liz Oliveira, Marcos Cardoso Martins Junior and Rodrigo Kandler

Centro de Ciências Agroveterinárias, Universidade do Estado de Santa Catarina, Av. Luiz de Camões, 2090, 88520-000, Lages, Santa Catarina, Brazil.
*Author for correspondence. E-mail: lucieli.leolato@gmail.com

ABSTRACT. Water deficiency reduces leaf expansion and photosynthetic efficiency, potentially reducing the ability to withstand leaf area (LA) loss. This study aimed to evaluate the effects of water restriction on soybean tolerance to defoliation in the vegetative and reproductive periods of development. Two experiments were conducted in a greenhouse located in Lages, Santa Catarina State Brazil, during the 2017/2018 growing season. Cultivar NA 5909 RG was subjected to three WR levels (none, moderate, and severe) and five defoliation levels (0, 17, 33, 50, and 67%). Defoliation occurred at the V6 stage in the first experiment and R3 in the second. WR occurred for 7 days after defoliation. LA at R2 and R5 after defoliation at V6 and R3 decreased by 27.5 and 64.6%, respectively, regardless of WR. LA between V6 and R2 was not influenced by WR or defoliation. Moderate or severe WR reduced plant ability to recover LA between R3 and R5. Severe WR decreased grain production by 22.2% in the vegetative period and 21.2% per plant in the reproductive period compared to that of the control, regardless of defoliation. The highest defoliation level reduced grain production per plant by 24.7 and 24.3% relative to the control at stages V6 and R3, respectively, regardless of WR. WR imposed at the vegetative and reproductive stages did not increase defoliation sensitivity.

Keywords: *Glycine max*; morphological characteristics; grain production; abiotic stress; leaf area.

Received on September 4, 2020.
Accepted on January 22, 2021.

Introduction

The productive performance of soybean depends on the genetic potential of the cultivars and the factors that interfere with the photosynthetic activity of the plant. Photosynthesis is affected by both biotic and abiotic stresses. Among them, defoliating insects and water deficiency reduce leaf area and photosynthetic rates of plants. This can result in grain yield losses, depending on the stage of crop development (Board & Kahloon, 2011).

Soybeans need a leaf area index close to 4.0 to achieve productivity higher than 4,000 kg ha^{-1} (Tagliapietra et al., 2018). However, the leaf area index can reach values higher than 8.0, depending on crop management conditions (Zanon et al., 2015a). Thus, soybeans can tolerate a certain defoliation level without a significant decrease in grain yield (Hoffmann-Campo, Corrêa-Ferreira, & Moscardi, 2012).

The control of defoliating insects, such as the soybean looper *Chrysodeixis includens* Walker, 1858 (Lepidoptera, Noctuidae) and the velvet bean caterpillar *Anticarsia gemmatalis* Hübner, 1818 (Lepidoptera, Noctuidae), should begin when the economic injury level reaches 30% defoliation during the vegetative period and 15% during the reproductive period. Additionally, integrated pest management practices recommend monitoring the population density of insects using a beat sheet, and considering the need for chemical intervention if the presence of up to 20 caterpillars (> 1.5 cm) per meter is observed (Bortolotto et al., 2015).

Several studies have attempted to elucidate the tolerance of soybeans to defoliation at different defoliation levels and crop development stages. The results have ranged from no reduction to a 68% decrease in grain yield (Bahry et al., 2013a and b; Glier et al., 2015; Zuffo et al., 2015; Monteiro et al., 2017; Durli et al., 2020), reinforcing the need for further research on this subject.

The effects of defoliation depend on the percentage of defoliation, injury duration, and stage of crop development (Hoffmann-Campo et al., 2012). However, under conditions of low productivity and unfavorable climatic conditions, defoliation is not the only yield-limiting factor that can aggravate losses in the productive performance of the crop.

All considered, there is a lack of information regarding the effect of defoliation under limiting environmental conditions during crop growth and development, such as those arising during water deficits. Therefore, a study to determine the combination of different types of stress that can trigger complex responses involving antagonistic effects and synergistic interactions in plant metabolism is necessary (Silva et al., 2010).

When soil moisture decreases, water retention by organic and inorganic colloids in the soil increases. This hinders water absorption by the root system, decreasing turgor pressure and the ability of plants to expand new leaves (Taiz, Zeiger, Møller, & Murphy, 2017). Therefore, soybean crops subjected to drought may have a higher sensitivity to defoliation because of their decreased leaf regeneration capacity after water stress.

This study was conducted to test the hypothesis that the tolerance of soybeans to defoliation is influenced by the soil moisture level, which is lower when the plant is subjected to water restriction. This hypothesis was based on the premise that plants under water stress reduce their leaf area and photosynthetic rate, limiting vegetative compensation and leaf recovery capacity of the crop after defoliation. The objective of this study was to evaluate the effects of water restriction on soybean tolerance to defoliation during the vegetative and reproductive periods of development.

Material and methods

Two experiments were conducted in a greenhouse located in Lages, Santa Catarina State, Brazil, during the 2017/2018 growing season. The greenhouse was maintained at a mean temperature of 25°C and relative humidity of approximately 70%.

The experimental design was randomized blocks in a 3 × 5 factorial scheme, with three replications, totaling 45 experimental units per experiment. Each experimental unit consisted of a polyethylene pot with a 5 L capacity. Three water restriction levels were tested: no restriction, moderate restriction, and severe restriction, in which soil moisture was maintained at 90, 70, and 50% of its field capacity, respectively. Five defoliation levels were imposed for each water restriction level: 0, 17, 33, 50, and 67%. The defoliation was performed using scissors, and the leaflets of all trifoliate leaves of the plant were removed or cut longitudinally according to the level of each treatment, as shown in Figure 1. The 0% defoliation level was equivalent to the control, 17 and 33% were close to the economic injury levels proposed by integrated pest management for the reproductive and vegetative stages, respectively, and 50 and 67% were above the economic injury level during any stage of crop development.

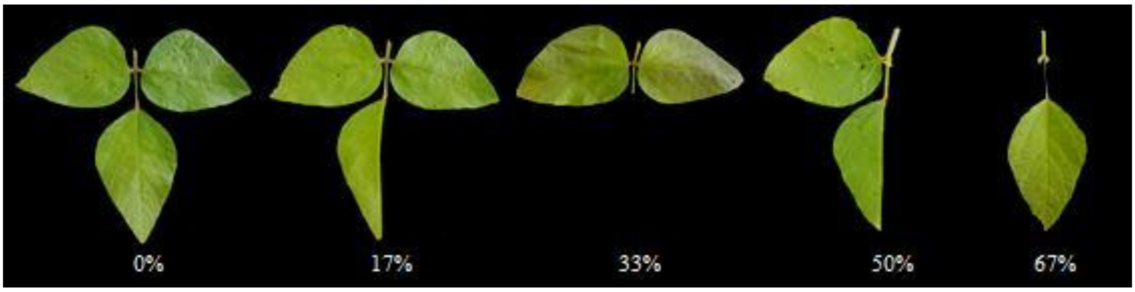

Figure 1. Defoliation levels imposed on each trifoliate soybean leaf.

In the first experiment, defoliation was performed at the V6 stage (six stem nodes with developed leaves). In the second experiment, defoliation was imposed at the R3 stage (beginning of pod formation), according to the phenological scale proposed by Fehr and Caviness (1977). The cultivar NA 5909 RG with a 5.9 maturation group, indeterminate growth habit, and substantial expressiveness of cultivated area in southern Brazil was used.

The water retention curve was determined by collecting soil using five stainless steel rings (3.0 cm high × 4.7 cm in diameter). A 100% viscose cloth was placed on one end of each ring and fixed externally with latex rubber. The samples were saturated in trays for approximately 24h by gradually increasing the water depth corresponding to 2/3 of the ring height.

The samples were submitted to a sand tension table at tensions of 1, 6, and 10 kPa and Richards chambers at tensions of 33, 100, 500, and 1,500 kPa (Richards, 1949). Subsequently, the samples were transferred to an oven at 105°C for 24h. The values of the wet mass of the soil under each tension step and the dry soil, together with the tare (aluminum ring, cloth, and rubber), were used to determine the field capacity and the permanent wilting point of the soil via gravimetric moisture (kg kg^{-1}). The soil field capacity was 32%, and the permanent wilting point was 18% moisture. Thus, 28.8, 22.4, and 16.0% gravimetric moisture corresponded to 90, 70, and 50% of the soil field capacity, characterizing the treatments with no water restriction, moderate water restriction, and severe water restriction, respectively, because the reduction in water content of plant leaves is proportional to the decrease in soil moisture (Fioreze, Rodrigues, Carneiro, Silva, & Lima, 2013).

The soil was maintained at a moisture level of 90% of the field capacity through daily irrigation until defoliation was conducted. Irrigation was suspended after defoliation at V6 or R3 in each experiment for the pots corresponding to moderate and severe water restriction, until the desired moisture level was attained in each treatment. The water restriction levels were maintained for 7 days after reaching the appropriate moisture, and the water replacement was calculated using the daily difference in pot weight. After this period, regular irrigation was resumed in all experimental units, maintaining soil moisture at 90% of the field capacity up to the R7 stage (grain physiological maturity) of the Fehr and Caviness (1977) scale.

Both experiments began on October 31, 2017, using five seeds per pot. Each pot was filled with a previously sieved dystrophic Red Nitosol. The soil had the following characteristics at a depth of 0 to 20 cm: 430 g kg^{-1} clay; pH in water 5.4; 36.7 mg dm^{-3} P; 217 mg dm^{-3} K; 3.8 g kg^{-1} organic matter; 5.9 $cmol_c$ dm^{-3} Ca; 2.8 $cmol_c$ dm^{-3} Mg; 0.1 $cmol_c$ dm^{-3} Al; and 14.5 $cmol_c$ dm^{-3} CEC.

The seeds were treated with 2 mL kg^{-1} of cyantraniliprole + thiamethoxam (Fortenza Duo®) and 3 mL kg^{-1} of inoculant (Masterfix L). Base fertilization consisted of 2 g of triple superphosphate and 2 g of potassium chloride per pot, following the recommendation of the Comissão de Química and Fertilidade do Solo (2016) to obtain a grain yield of 6,000 kg ha^{-1}. Thinning was conducted when the plants were in the V1 stage to maintain one plant per pot.

Disease control was performed using 1 g L^{-1} of azoxystrobin + benzovindiflupyr (Elatus®) and 2.6 mL L^{-1} of trifloxystrobin + prothioconazole (Fox®) at stages V5 and R5, respectively. Pest control was performed with 1.2 mL L^{-1} of profenophos + lufenuron (Curyom®), 0.5 mL L^{-1} of lambda-cyhalothrin + chlorantraniliprole (Ampligo®), 1 mL L^{-1} of thiamethoxam + lambda-cyhalothrin (Engeo Pleno®), and 0.5 ml L^{-1} of flufenoxuron (Cascade®) at stages V2, V4, V6, and R1, respectively.

The leaf area was determined by measuring the length and the largest width of the central leaflets of each trifoliate leaf of the plant and applying the equation proposed by Richter et al. (2014): $LA = a \times (L \times W)$, where LA is the leaf area (cm^2), L is the leaf length (cm), W is the largest leaf width (cm), and a is the angular coefficient (2.0185). The first leaf area evaluation was performed on the day of defoliation in each experiment. The second leaf area evaluation was conducted at stages R2 (full bloom) and R5 (beginning of grain filling) in the experiments with defoliation at V6 and R3, respectively. The difference in leaf area between V6 and R2 in the experiment with defoliation at V6, and that between R3 and R5 in the experiment with defoliation at R3 were also determined.

Soybean harvest was conducted on April 2nd, 2018. The following evaluations were performed after harvest: grain production per plant, thousand-grain weight, number of pods per plant, and number of grains per pod. The data were subjected to an analysis of variance using the F-test at a 5% significance level ($p < 0.05$). When the significance levels were reached, the means of the qualitative factor (water restriction) were compared using the Tukey test and those of the quantitative factor (defoliation) were compared by polynomial regression, both at a 5% significance level ($p < 0.05$). Linear and quadratic equations in the figures were chosen according to the coefficient of determination that best fit the tested models.

Results and discussion

Table 1 shows the F values and their significance levels for the variables analyzed during the experiment. There was no significant interaction between water restriction and defoliation levels for the studied variables.

The leaf area measured before defoliation was 793 cm^2 at the V6 stage in the first experiment and 4,020 cm^2 at the R3 stage in the second experiment. The leaf areas at R2 and R5, corresponding to the experiments at V6 and R3, respectively, were influenced by defoliation (Table 1). A linear reduction in the leaf area was observed as the percentage of defoliation increased, with a 27.5% and 64.6% decrease in the highest defoliation level compared to that of the control at stages V6 and R3, respectively (Figure 2A and B).

Each 10% of leaf area removed at V6 and R3 led to a reduction in leaf area of 85.9 and 421.0 cm^2 at R2 and R5, respectively. The leaf area values measured in the R5 stage were higher, and the decrease rates because of defoliation were more pronounced. This occurred because most of the new leaves are produced up until the beginning of pod formation in cultivars with indeterminate growth habits (Zanon et al., 2015a).

Table 1. F values according to the analysis of variance for the variables of leaf area at R2 and R5 (LA1) and leaf area between V6 and R2 and that between R3 and R5 (LA2), grain production per plant (GPP), thousand-grain weight (TGW), number of pods per plant (NPP), and number of grains per pod (NGP) as a function of the three water restriction levels (no restriction, moderate, and severe)[1/] and five defoliation levels (0, 17, 30, 50, and 67%) at stages of development V6 and R3[2/].

Source of variation[3/]	DF	LA1	LA2	GPP	TGW	NPP	NGP
Experiment with defoliation at V6							
Water restriction (WR)	2	2.5 ns[3/]	0.2 ns	8.2**	8.0**	7.3*	1.6 ns
Defoliation (D)	4	4.0**	2.4 ns	4.8**	8.5**	0.41 ns	1.8 ns
WR × D	8	1.1 ns	1.2 ns	0.9 ns	1.3 ns	1.58 ns	0.6 ns
Blocks	2	0.6 ns	0.9 ns	1.8 ns	10.0**	3.71*	2.7 ns
Residual	28						
Total	44						
Experiment with defoliation at R3							
Water restriction (WR)	2	0.7 ns	4.6*	11.9**	7.9**	43.8*	15.8**
Defoliation (D)	4	64.8**	1.0 ns	5.6**	0.5 ns	6.43*	1.5 ns
WR × D	8	0.9 ns	1.3 ns	0.4 ns	1.0 ns	1.1 ns	0.5 ns
Blocks	2	3.7*	6.8**	0.05 ns	10.9**	10.3**	1.9 ns
Residual	28						
Total	44						

[1/]No restriction: 90% of the soil field capacity; moderate: 70% of the soil field capacity; severe: 50% of the soil field capacity. [2/]Stages according to the phenological scale proposed by Fehr and Caviness (1977): V6 (six stem nodes with fully developed leaves), R2 (full bloom), R3 (beginning of pod formation), and R5 (beginning of grain filling). [3/]**Significant at the 1% probability level ($p < 0.01$); *significant at the 5% probability level ($p < 0.05$); ns, non-significant ($p > 0.05$).

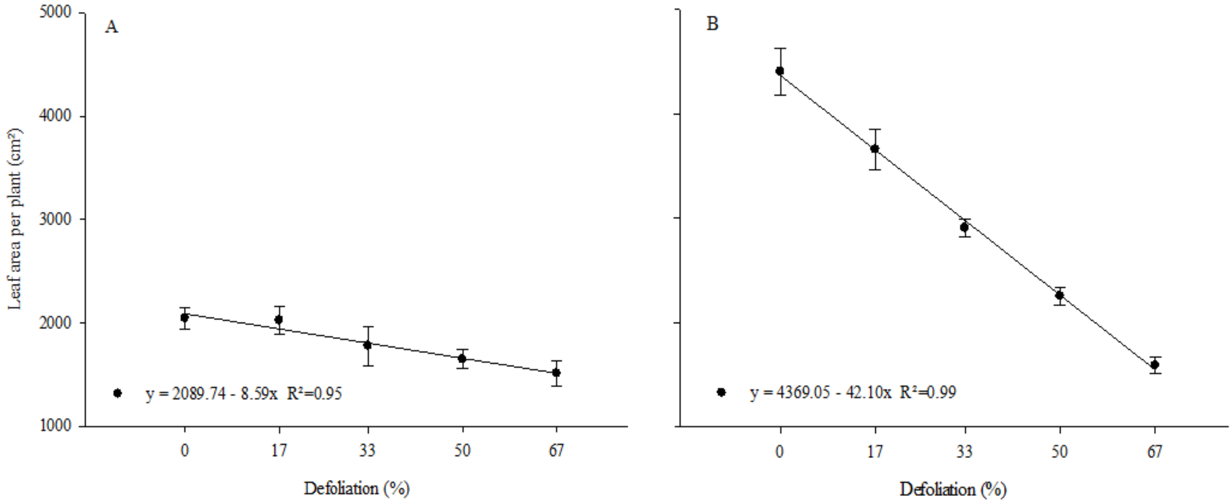

Figure 2. Leaf area per soybean plant at stages R2 (full bloom) (A) and R5 (beginning of grain filling) (B) as a function of defoliation at stages V6 (six stem nodes with fully developed leaf) and R3 (beginning of pod formation), considering three water restriction levels (90, 70, and 50% of the soil field capacity). Lages, Santa Catarina State, Brazil, 2017/2018 season. Bars indicate the treatment mean ± standard error.

The leaf area between stages V6 and R2 varied from 251 to 1697 cm^2 and was not affected by water restriction or defoliation (Table 1). This result corroborates with Durli et al. (2020), who also reported that the leaf area between stages V6 and R2 was not influenced by defoliation at the V6 stage, regardless of the maturation group of the cultivar.

The absence of a significant effect of treatments on this variable, despite the large numerical differences, is associated with the high value of the least significant difference between means caused by a coefficient of variation of 49%. The least significant difference was 465 for water restriction and 709 for defoliation. Thus, defoliation and water restriction had no influence on plant capacity for leaf offsetting from V6 to R2.

The leaf area per plant between R3 and R5 was influenced by water restriction (Table 1). Both moderate and severe water restrictions reduced the ability of plants to produce new leaves (Table 2).

The reduction of leaf area with an increase in water restriction is one of the first plant reactions in response to a water deficit. It is a morphophysiological mechanism that balances water conservation by plants and the CO_2 assimilation rate for carbohydrate production (Taiz et al., 2017).

Table 2. Leaf area per soybean plant between stages R3 and R5, grain production, thousand-grain weight, number of pods per plant, and number of grains per soybean pods as a function of water restriction at the V6 and R3 stages of development, considering the average of five defoliation levels1/. Lages, Santa Catarina State, Brazil, 2017/2018 season.

	Water restriction level2/			CV (%)
	No restriction	Moderate	Severe	
V6 stage3/				
Grain production (g)	36.6 a*	33.3 ab	28.4 b	16.8
Thousand-grain weight (g)	177.1 a	169.9 a	152.8 b	10.2
Pods per plant	89.7 a	85.6 ab	78.1 b	9.9
R3 stage				
Leaf area (R3–R5) (cm^2)	361 a*	226 b	242 b	47.5
Grain production (g)	33.9 a	32.9 a	26.7 b	14.1
Thousand-grain weight (g)	191.6 a	176.9 ab	164.2 b	10.6
Pods per plant	84.6 a	74.4 b	58.0 c	10.8
Grains per pod	2.72 a	2.61 b	2.47 c	4.7

1/Defoliation levels: 0, 17, 30, 50, and 67%. 2/No restriction: 90% of the soil field capacity; moderate: 70% of the soil field capacity; severe: 50% of the soil field capacity. 3/Stages according to the phenological scale proposed by Fehr and Caviness (1977): V6 (six stem nodes with fully developed leaves), R3 (beginning of pod formation), and R5 (beginning of grain filling). *Means followed by different lowercase letters in a row differ from each other according to the Tukey test at the 5% significance level.

Defoliation had no significant effect on the leaf area between V6 and R2 and between R3 and R5, regardless of the phenological stage at which it was performed and soil moisture level (Table 1). The theoretical expectation was that the plants would have a high capacity to expand new leaves in treatments with high defoliation and no water deficiency. Cell turgor is higher in well-hydrated plants, which favors leaf expansion because the turgor pressure pushes the plasma membrane against the rigid cell wall and provides strength for cell extension (Taiz et al., 2017).

Grain production per plant was influenced by water restriction and defoliation in both experiments (Table 1). Grain production per plant decreased with increased water restriction at both development stages (Table 2). This reduction reached 8.2 and 7.2 g relative to that of the control, representing a decrease of 22.2 and 21.2% at stages V6 and R3, respectively. The reduction in grain production was similar in both stages of development, in contrast to the behavior observed by Mertz-Henning et al. (2018), where the authors found a higher effect of water deficit when stress was imposed during the reproductive period. The reduction in grain yield was approximately 33 and 67% at the vegetative and reproductive stages, respectively, during the three growing seasons of the field experiments.

The lower effect of water restriction on grain production per plant during the reproductive period also differed from the results reported by Nunes et al. (2016) and Giordani et al. (2019). Although water is essential throughout the crop cycle, the reproductive period is the most critical, as water deficit during the vegetative stages can be mitigated by subsequent precipitation throughout development (Mundstock & Thomas, 2005). This response may be associated with the environmental conditions of the greenhouse during water restriction imposition (Table 3).

Table 3. Maximum, minimum, and mean values of temperature and relative humidity in the greenhouse during the period of water restriction imposition during stages V6 and R3 of soybean development.

	Air temperature (°C)			Relative air humidity (%)		
Stage of development	Minimum	Maximum	Mean	Minimum	Maximum	Mean
V6 1/	19.2	40.8	27.0	27.8	93.0	67.4
R3	18.6	37.9	25.3	36.2	97.5	75.5

1/Means from 11/12/17 to 11/24/17 for the vegetative period and 1/5/18 to 1/16/18 for the reproductive period. Stages according to the phenological scale proposed by Fehr and Caviness (1977): V6 (six stem nodes with fully developed leaves) and R3 (beginning of pod formation).

The mean temperature was 1.7°C higher during water restriction imposition in the vegetative period relative to that in the reproductive period. Although the increase in temperature was punctual, Zhang, Zhu, Yu, and Zhong (2016) also found that an increase of 1.8°C at the bloom stage reduced the productive performance of the crop. These decreases were 45% in grain yield, 20.8% in grain weight, and 41% in the harvest index.

Therefore, a lower temperature and higher relative humidity of the air during water restriction imposition during the reproductive period indicated that the stress was probably less severe at this stage of development. The higher the temperature and the lower the relative humidity of the air, the more accentuated is the evaporative demand of the atmosphere and the more intense the damages caused by water deficiency to plants could be (Teixeira, Beltrão, & Evangelista, 2011).

Additionally, cultivars with indeterminate growth habits have an extended period of overlap between the vegetative and reproductive stages (Zanon et al., 2015b), which may have mitigated the effects of water deficit at the R3 stage. Moreover, the productive stability of the cultivar NA 5909 RG has been reported under different cultivation conditions (Matei et al., 2017; Câmara, Moraes, & Simon, 2018; Bicalho et al., 2019). It also contributed to similar grain production losses with a severe water deficit in the vegetative and reproductive periods.

Grain production per plant decreased quadratically as the defoliation percentage increased in both experiments (Figure 3A and B). The defoliation performed at V6 led to a reduction of 9.1 g in grain production per plant with 67% defoliation, representing a decrease of 24.7% relative to that of the control. The defoliation performed at R3 led to a reduction of 8.3 g in grain production per plant with 67% defoliation, representing a decrease of 24.3% relative to that of the control.

Monteiro et al. (2017) reported a similar result, observing that grain production per plant decreased with 25% defoliation at the V6 stage and R2 stage of development in an indeterminate growth habit cultivar. Glier et al. (2015) also found a reduction in grain yield with 25% defoliation at stages V9, R3, and R5. However, the highest losses occurred during the reproductive period of development.

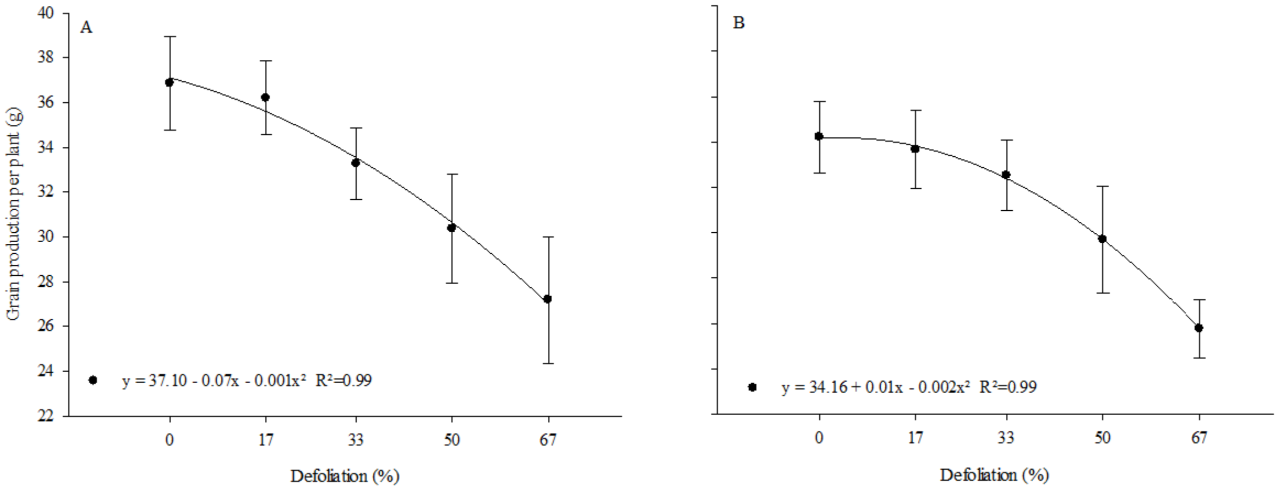

Figure 3. Grain production per soybean plant as a function of defoliation at stages V6 (six stem nodes with fully developed leaf) (A) and R3 (beginning of pod formation) (B), considering an average of three water restriction levels (90, 70, and 50% of the soil field capacity). Lages, Santa Catarina State, Brazil, 2017/2018 season. Bars indicate the treatment mean ± standard error.

According to Board and Kahloon (2011), the leaves remaining after defoliation do not photosynthetically compensate for losses. Thus, a loss in leaf area will reduce the plant photosynthetic rate and decrease the production of photoassimilates and grain yield, as observed in the present study. However, a higher effect of defoliation on grain production per plant was expected to occur during the reproductive period than that during the vegetative period, but such was not observed. This behavior may be associated with the offsetting effect between yield components. The reduction of only one yield component through defoliation at each stage (thousand-grain weight at V6 and number of pods per plant at R3) meant that, in the end, defoliation effects on grain production per plant were similar for the two development periods (Figure 4A and B).

This study showed that soybeans are sensitive to water deficits during the vegetative and reproductive stages of development (Table 2). Likewise, soybeans are affected by the loss of leaf area because there was a reduction in grain production per plant with a defoliation level considered low (17%) (Figure 3). However, water restriction did not affect defoliation. Therefore, the effects of these factors on soybean production performance were independent and additive. This behavior did not confirm the hypothesis of the study that the tolerance of soybeans to defoliation is lower in plants subjected to water restriction.

Similar to the present study, Grinnan, Carter, and Johnson (2013a, 2013b) also observed no interaction between natural defoliation and water deficit in soybean production performance in experiments conducted under controlled and field conditions. Therefore, the authors concluded that the effects of these stressors could be independently studied.

The thousand-grain weight was influenced by water restriction in both experiments and by defoliation at V6 (Table 1). It decreased with a severe restriction at both development stages (Table 2). The reduction in grain mass at V6 and R3 occurred because the lack of water changes the balance between vegetative and reproductive growth at any development stage (Mundstock & Thomas, 2005). However, Mertz-Henning et al. (2018) and Giordani et al. (2019) found that a reduction in grain weight because of water deficit during the vegetative and reproductive stages occurred only in some cultivars, showing the importance of genotype characteristics in response to this type of stress.

The thousand-grain weight decreased linearly as the percentage of defoliation at the V6 stage increased (Figure 4A). A 5.7 g in grain weight reduction was verified for each 10% of leaf area removed. The highest defoliation level reduced thousand-grain weight by 38.1 g, representing a decrease of 20.6% compared to that of the control. It was the only yield component influenced by the defoliation at the V6 stage

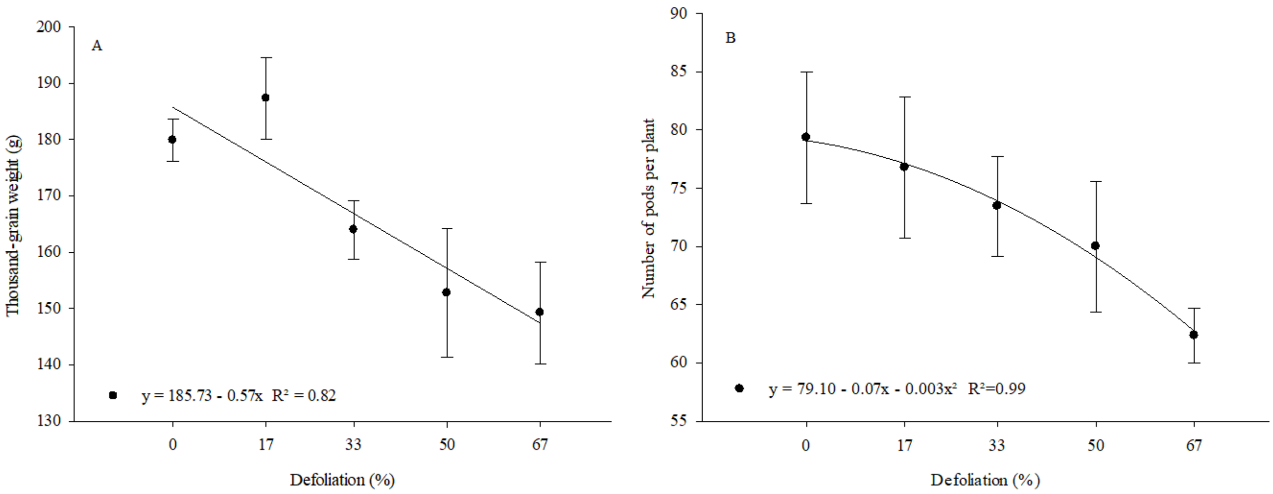

Figure 4. Thousand-grain weight as a function of defoliation at V6 (six stem nodes with fully developed leaf) (A) and the number of pods per soybean plant as a function of defoliation at R3 (beginning of pod formation) (B), considering an average of three water restriction levels (90, 70, and 50% of the soil field capacity). Lages, Santa Catarina State, Brazil, 2017/2018 season, Brazil. Bars indicate the treatment mean ± standard error.

A similar result was also reported by Bahry et al. (2013b), who found a reduction in grain weight with increasing defoliation up to 66.7% between stages V4 and V9, with the lowest value obtained with the highest defoliation level. The authors concluded that the reduction in grain weight caused by defoliation was directly related to a limitation in leaf area, which resulted in lower production of photoassimilates for grain filling.

The thousand-grain weight was not influenced by defoliation at the R3 stage (Table 1). The theoretical expectation was that there would be a higher impact of leaf area loss at the reproductive stage on this variable, but this did not occur. This response was associated with the compensation that exists between yield components. In this sense, the number of pods per plant was negatively affected by defoliation only at R3 (Figure 4B). With a low number of pods to fill, the plant maintained the grain weight when defoliated.

The number of pods per plant was influenced by water restriction in both experiments and defoliation at R3 (Table 1). Only severe restriction reduced the number of pods per plant when applied at V6 (Table 2). Both moderate and severe restrictions reduced this variable when applied at R3. Nunes et al. (2016) also reported a reduction in the number of pods per plant with severe water deficit imposition at the two stages of crop development and the imposition of moderate water deficit at the reproductive stage.

The reduction in the number of pods when the water deficit occurs during the vegetative period is caused by lower plant height, a smaller number of stem nodes, and fewer branches. An alteration promotes these morphological changes in the growth balance as a function of the restriction of photoassimilates (Mundstock & Thomas, 2005). The number of pods was reduced when the water deficit occurred during blooming and the beginning of pod formation because of the higher rate of flower and pod abortion. However, grain size and weight were reduced during the grain filling stage (Ekhtiari, Kobraee, & Shamsi, 2013).

The number of pods per plant decreased quadratically as the percentage of defoliation at R3 increased (Figure 4B). There was a reduction of 18.1 pods per plant with the highest defoliation level, representing a decrease of 22.9% compared to that of the control. This result was also observed by Durli et al. (2020), who verified a reduction in the number of pods per plant with increasing defoliation at the beginning of pod formation in the cultivars NA 5909 RG and TMG 7262 RR.

The reduction in leaf area negatively influences the yield components because of a decrease in the amount of photoassimilates produced by the plant (Schmildt, Amaral, Pratissoli, & Reis, 2010). Thus, the plant aborts part of the pods and keeps those that can translocate photoassimilates from the remaining leaves (Silva et al., 2015).

The number of grains per pod ranged from 2.5 to 2.8. It was not influenced by water restriction or defoliation at the V6 stage (Table 1). However, this variable was affected by water restriction at the R3 stage, which decreased with an increase in water restriction (Tables 1 and 3). The association of the two types of stress (water restriction and defoliation) at the reproductive stage may have accentuated the source restriction in the plant, reducing the number of grains per pod, a characteristic that is usually not influenced by environmental growth conditions (Silva et al., 2015).

Conclusion

Water restriction of 50% of the soil field capacity for 7 days in a greenhouse reduced grain production per plant of the cultivar NA 5909 RG at the vegetative and reproductive stages, regardless of the defoliation level. The increase in defoliation percentage from 17 to 67% at V6 and R3 reduced grain production per plant of the cultivar NA 5909 RG in a greenhouse, regardless of the soil moisture level. Water restriction imposition at the vegetative and reproductive stages did not increase the sensitivity to defoliation of the cultivar NA 5909 RG grown in a greenhouse.

Acknowledgements

To UNIEDU/FUMDES for granting the doctoral fellowship to the first author. To CNPq for granting a research productivity fellowship to the second author. To FAPESC for granting financial support (Term of Grant 2019TR639 FAPESC/PAP/UDESC).

References

Bahry, C. A., Venske, E., Nardino, M., Zimmer, P. D., Souza, V. Q., & Caron, B. O. (2013a). Desempenho agronômico da soja em função da desfolha em diferentes estádios vegetativos. *Tecnologia e Ciência Agropecuária*, *7*(4), 19-24.

Bahry, C., Dantas, E., Venske, E., Nardino, M., Zimmer, P., Souza, V., & Caron, B. (2013b). Efeito da desfolha na fase vegetativa em alguns caracteres agronômicos da cultivar de soja BMX Potência RR. *Revista de Agricultura*, *88*(3), 179-184. DOI: https://doi.org/10.37856/bja.v88i3.110

Bicalho, T. F., Nogueira, A. P. O., Hamawaki, O. T., Costa, S. C., Morais Júnior, I. J., Silva, N. S., ... Hamawaki, C. D. L. (2019). Adaptability and stability of soybean cultivars in four sowing seasons. *Bioscience Journal*, *35*(5), 1450-1462. DOI: https://doi.org/10.14393/BJ-v35n5a2019-42351

Board, J. E., & Kahlon, C. S. (2011). Soybean yield formation: What controls it and how it can be improved. In H. A. El-Shamy (Ed.), *Soybean physiology and biochemistry* (p. 1-36). London, UK: IntechOpen.

Bortolotto, O. C., Pomari-Fernandes, A., Bueno, R. C. O. F., Bueno, A. F., Cruz, Y. K. S, Sanzovo, A., & Ferreira, R. B. (2015). The use of soybean integrated pest management in Brazil: A review. *Agronomy Science and Biotechnology*, *1*(1), 25-32. DOI: https://doi.org/10.33158/ASB.2015v1i1p25

Câmara, A. R., Moraes, R. N. O., & Simon, G. A. (2018). Adaptabilidade e estabilidade de genótipos de soja nos estados de Goiás e Minas Gerais. *Global Science and Technology*, *11*(2), 23-36.

Comissão de Química e Fertilidade do Solo. (2016). *Manual de adubação e calagem para os estados do Rio Grande do Sul e de Santa Catarina*. Porto Alegre, RS: Sociedade Brasileira de Ciência do Solo.

Durli, M. M., Sangoi, L., Souza, C. A., Leolato, L. S., Turek, T. L., & Kuneski, H. K. (2020). Defoliation levels at vegetative and reproductive stages of soybean cultivars with different relative maturity groups. *Revista Caatinga*, *33*(2), 30-45. DOI: https://doi.org/10.1590/1983-21252020v33n213rc

Ekhtiari, S., Kobraee, S., & Shamsi, K. (2013). Soybean yield under water deficit conditions. *Journal of Biodiversity and Environmental Sciences*, *3*(2), 46-52.

Fehr, W. R., & Caviness, C. E. (1977). *Stages of soybean development*. Ames, IA: Iowa State University.

Fioreze, S. L., Rodrigues, J. D., Carneiro, J. P. C., Silva, A. A., & Lima, M. B. (2013). Fisiologia e produção da soja tratada com cinetina e cálcio sob deficit hídrico e sombreamento. *Pesquisa Agropecuária Brasileira*, *48*(11), 1432-1439. DOI: https://doi.org/10.1590/S0100-204X2013001100003

Giordani, W., Gonçalves, L. S. A., Moraes, L. A. C., Ferreira, L. C., Neumaier, N., Farias, J. R. B., … Henning, L. M. M. (2019). Identification of agronomical and morphological traits contributing to drought stress tolerance in soybean. *Australian Journal of Crop Science*, *13*(1), 35-44. DOI: https://doi.org/10.21475/ajcs.19.13.01.p1109

Glier, C. A. S., Duarte Júnior, J. B., Fachin, G. M., Costa, A. C. T., Guimarães, V. F., & Mrozinski, C. R. (2015). Defoliation percentage in two soybean cultivars at different growth stages. *Revista Brasileira de Engenharia Agrícola e Ambiental*, *19*(6), 567-573. DOI: https://doi.org/10.1590/1807-1929/agriambi.v19n6p567-573

Grinnan, R., Carter, T. E., & Johnson, M. T. J. (2013a). Effects of drought, temperature, herbivory, and genotype on plant–insect interactions in soybean (*Glycine max*). *Arthropod-Plant Interactions*, *7*(2), 201-215. DOI: https://doi.org/10.1007/s11829-012-9234-z

Grinnan, R., Carter, T. E., & Johnson, M. T. J. (2013b). The effects of drought and herbivory on plant–herbivore interactions across 16 soybean genotypes in a field experiment. *Ecological Entomology*, *38*(3), 290-302. DOI: https://doi.org/10.1111/een.12017

Hoffmann-Campo, C. B., Corrêa-Ferreira, B. S., & Moscardi, F. (2012). *Soja: Manejo integrado de pragas e outros artrópodes-praga*. Brasília, DF: Embrapa.

Matei, G., Benin, G., Woyann, L. G., Dalló, S. C., Milioli, A. S., & Zdziarski, A. D. (2017). Agronomic performance of modern soybean cultivars in multi-environment trials. *Pesquisa Agropecuária Brasileira*, *52*(7), 500-511. DOI: https://doi.org/10.1590/s0100-204x2017000700004

Mertz-Henning, L. M., Ferreira, L., Henning, F., Mandarino, J., Santos, E., Oliveira, M., … Neumaier, N. (2018). Effect of water deficit-induced at vegetative and reproductive stages on protein and oil content in soybean grains. *Agronomy*, *8*(1), 1-11. DOI: https://doi.org/10.3390/agronomy8010003

Monteiro, M. A., Koch, F., Nobre, F. L. L., Zulli, F. S., Araújo, B. O. N., Borges, E. G., . . . Santos, E. L. (2017). Intensidade de desfolha e desempenho de plantas de soja com diferentes hábitos de crescimento. *Scientia Agraria Paranaensis*, *16*(2), 265-269. DOI: https://doi.org/10.18188/1983-1471/sap.v16n1p265-269

Mundstock, C. M., & Thomas, A. L. (2005). *Soja: Fatores que afetam o crescimento e o rendimento de grãos*. Porto Alegre, RS: Evangraf.

Nunes, A. C., Bezerra, F. M. L., Silva, R. Ae, Silva Júnior, J. L. Cd, Gonçalves, F. B., & Santos, G. A. (2016). Agronomic aspects of soybean plants subjected to deficit irrigation. *Revista Brasileira de Engenharia Agrícola e Ambiental*, *20*(7), 654-659. DOI: https://doi.org/10.1590/1807-1929/agriambi.v20n7p654-659

Richards, L. A. (1949). Methods of measuring soil moisture tension. *Soil Science*, *68*(1), 95-112. DOI: https://doi.org/10.1097/00010694-194907000-00008

Richter, G. L., Zanon Júnior, A., Streck, N. A., Guedes, J. V. C., Kräulich, B., Rocha, T. S. Md, … Cera, J. C. (2014). Estimativa da área de folhas de cultivares antigas e modernas de soja por método não destrutivo. *Bragantia*, *73*(4), 416-425. DOI: https://doi.org/10.1590/1678-4499.0179

Schmildt, E. R., Amaral, J. A. T., Pratissoli, D., & Reis, E. F. (2010). Influência de desfolhas artificiais para simular perdas na produção do feijoeiro (*Phaseolus vulgaris* L. Cv. Xamego). *Arquivos do Instituto Biológico*, *77*(3), 457-463. DOI: https://doi.org/10.1590/1808-1657v77p4572010

Silva, E. N., Ferreira-Silva, S. L., Fontenele, A. V., Ribeiro, R. V., Viégas, R. A., & Silveira, J. A. G. (2010). Photosynthetic changes and protective mechanisms against oxidative damage subjected to isolated and combined drought and heat stresses in *Jatropha curcas* plants. *Journal of Plant Physiology*, *167*(14), 1157-1164. DOI: https://doi.org/10.1016/j.jplph.2010.03.005

Silva, A. F., Sediyama, T., Silva, F. C., Bezerra, A. R. G., Borém, A., Ferreira, L. V., … Barros, J. P. A. (2015). Continuous defoliation stress in vegetative and reproductive stages of soybean genotypes. *Journal of Agronomy*, *14*(4), 279-285. DOI: https://doi.org/10.3923/ja.2015.279.285

Tagliapietra, E. L., Streck, N. A., Rocha, T. S. M., Richter, G. L., Silva, M. R., Cera, J. C., … Zanon, A. J. (2018). Optimum leaf area index to reach soybean yield potential in subtropical environment. *Agronomy Journal*, *110*(3), 932-938. DOI: https://doi.org/10.2134/agronj2017.09.0523

Taiz, L., Zeiger, E., Møller, I. M., & Murphy, A. (2017). *Fisiologia e desenvolvimento vegetal*. Porto Alegre, RS: Artmed.

Teixeira, G. C. S., Beltrão, D. S., & Evangelista, A. W. P. (2011). Estudos de evapotranspiração em casa de vegetação. *Enciclopédia Biosfera*, *7*(13), 520-530.

Zanon, A. J., Streck, N. A., Richter, G. L., Becker, C. C., Rocha, T. S. Md, Cera, J. C., ... Weber, P. S. (2015a). Contribuição das ramificações e a evolução do índice de área foliar em cultivares modernas de soja. *Bragantia*, *74*(3), 279-290. DOI: https://doi.org/10.1590/1678-4499.0463

Zanon, A. J., Winck, J. E. M., Streck, N. A., Rocha, T. S. M., Cera, J. C., Richter, G. L., ... Marchesan, E. (2015b). Desenvolvimento de cultivares de soja em função do grupo de maturação e tipo de crescimento em terras altas e terras baixas. *Bragantia*, *74*(4), 400-411. DOI: https://doi.org/10.1590/1678-4499.0043

Zhang, L., Zhu, L., Yu, M., & Zhong, M. (2016). Warming decreases photosynthates and yield of soybean [*Glycine max* (L.) Merrill] in the North China Plain. *Crop Journal*, *4*(2), 139-146. DOI: https://doi.org/10.1016/j.cj.2015.12.003

Zuffo, A. M.; Zambiazzi, E. V., Gesteira, G. S., Rezende, P. M., Bruzi, A. T., Soares, I. O., ... Bianchi, M. C. (2015). Agronomic performance of soybean according to stages of development and levels of defoliation. *African Journal of Agricultural Research*, *10*(19), 2089-2096. DOI: https://doi.org/10.5897/ajar2014.9369