Tolerance of Soybean to Defoliation at Pod Formation as Affected by Soil Fertility

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ABSTRACT

Nutrient deficiency reduces new leaf growth, leaf area duration, and photosynthetic activity. Such effects may enhance the sensitivity of soybean to defoliation. This study aimed to assess the effects of soil fertility on defoliation tolerance in soybean at the beginning of pod formation. A greenhouse experiment was conducted in Lages, Santa Catarina, Brazil, during the 2021/22 growing season. Two soil fertility conditions (high and low) and five defoliation levels (0, 17, 33, 50, and 67%) were tested. Defoliation was performed at the R3 stage. The soybean cultivar used was 'NA 5909 RG'. Leaf area at R3 and R5 was higher under high fertility conditions. At R5, leaf area decreased by 63.8% at the highest defoliation level compared with the control, regardless of soil fertility. Under high fertility conditions, there was a 12.9% increase in leaf area between R3 and R5 in the 67% defoliation treatment compared with the control. Grain yield was 24.7% higher in high fertility soil. An increase in the level of defoliation from 0 to 67% decreased grain yield per plant by 11.9% under both soil fertility conditions. These results suggest that a reduction in soil fertility does not increase defoliation sensitivity in soybean 'NA 5909 RG'.

Keywords: *Glycine max*, grain production, plant nutrition, leaf area.

INTRODUCTION

Nutrients perform essential functions at all stages of crop development. They can act directly, by participating in specific metabolic processes, or indirectly, by altering photosynthate and phytohormone concentrations (Engels et al., 2012). Nutrient absorption increases with the increase in nutrient availability, leading to improvements in total biomass production and grain yield (Gonçalves Júnior et al., 2010; Carvalho et al., 2012; Bender et al., 2015; Duarte et al., 2016; Yang and Zhangh, 2023; Rogers et al., 2024).

Abiotic and biotic stresses reduce photosynthesis, accelerate leaf senescence, and may decrease grain yield as a result of source limitation. Under stress conditions, nutrient reserves accumulated in vegetative organs during development become an important source of assimilates for grain filling (Engels et al., 2012; Hajibarat and Saidi, 2022; Poudel et al., 2025). Bender et al. (2015) found that two-thirds of the potassium accumulated in soybean resulted from remobilization of nutrients from stems and petioles.

Defoliation caused by biotic agents (e.g., caterpillars) and abiotic agents (e.g., hailstones) is one of the most common stressors in soybean. Two responses are commonly observed in plants that have undergone defoliation: (i) an increase in the photosynthetic capacity of remaining leaves and (ii) an increase in leaf growth rates (Briske and Richards, 1995). These physiological responses allow soybean to tolerate defoliation to a certain extent without showing a significant decrease in grain yield (Hoffmann-Campo et al., 2012, Leolato et al., 2022).

According to the premises of integrated pest management (IPM), strategies for the control of defoliating insects, such as the velvetbean caterpillar, *Anticarsia gemmatalis* Hübner, 1818 (Lepidoptera, Noctuidae), and the soybean looper, *Chrysodeixis includens* Walker, 1858 (Lepidoptera, Noctuidae), should be implemented when the economic injury level is reached (30% defoliation during the vegetative stage and 15%

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defoliation during the reproductive stage). In parallel, IPM recommends monitoring the population density of these insects by the beat cloth method; chemical intervention should be made when more than 20 caterpillars per meter (>1.5 cm) are sampled (Bortolotto et al., 2015).

Nutrient deficiency limits plants' ability to expand new leaves, reduces photosynthesis, and decreases leaf area duration and the time leaves act as sources of photoassimilates to sinks (Engels et al., 2012). Environmental factors, such as soil fertility, may influence the tolerance of soybean to defoliation (Boiça Júnior et al., 2015; Leolato et al., 2023). An experiment was conducted considering the hypothesis that soybean tolerance to leaf area reduction is lower in environments with low nutrient availability. The hypothesis was based on the fact that plants have smaller leaf areas and reduced photosynthetic activity when grown in low fertility soil, possibly limiting their ability to recover from defoliation. This study aimed to investigate the effects of soil fertility on the tolerance of soybean to defoliation at the beginning of pod formation.

MATERIAL AND METHODS

The experiment was conducted in a greenhouse in Lages (27º48’58” S, 50º19’34” W), southern plateau region of Santa Catarina State, Brazil, during the 2021/22 growing season. The greenhouse was maintained at a mean temperature of 25°C and relative air humidity of about 70%.

A 2 × 5 factorial randomized block design was used, with two levels of soil fertility (high and low), five levels of defoliation (0, 17, 33, 50, and 67%), and three replications per treatment, totaling 30 experimental units. Soybean plants were subjected to defoliation treatments at the R3 stage (beginning of pod formation), as assessed according to the phenological scale proposed by Fehr and Caviness (1977). Each experimental unit consisted of a 5 L polyethylene pot.

Defoliation was performed by using scissors. Leaflets of trifoliate leaves were removed or cut lengthwise according to each defoliation treatment, as illustrated below (Figure 1). A defoliation level of 0% was adopted as control. Foliage losses of 17 and 33% are close to the economic injury levels of soybean in the reproductive and vegetative phases, respectively. Defoliation levels of 50 and 67% are above the economic injury level for any phase of crop development. The soybean cultivar used was ‘NA 5909 RG’, which belongs to the 6.2 maturation group, exhibits an indeterminate growth habit, and has high representativeness of cultivated area in southern Brazil.

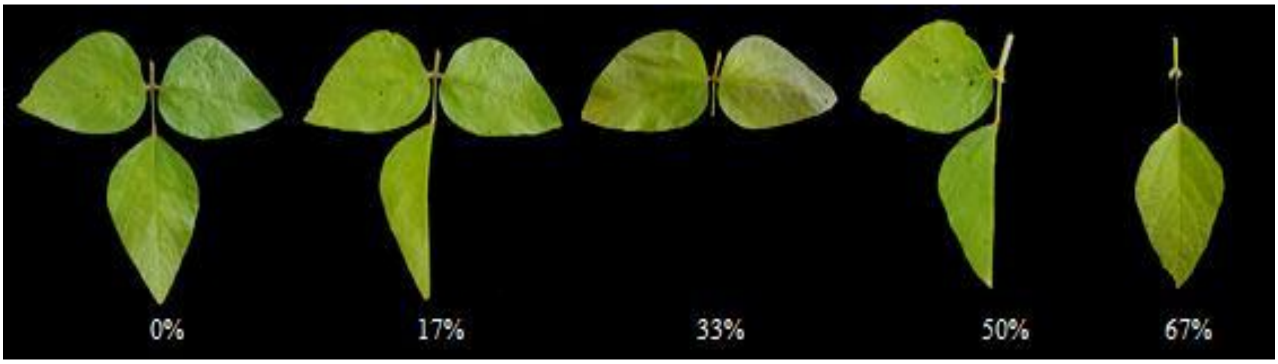


Figure 1. Defoliation levels applied to trifoliate leaves of soybean plants

The soil used in the experiment was classified as a dystrophic Red Nitosol. Physicochemical characterization of the 0 to 20 cm layer revealed the following parameters: 330 g dm^{-3} clay, pH (in water) of 4.8, 4.6 mg dm^{-3} P, 72 mg dm^{-3} K, 2.9 g dm^{-3} organic matter, 1.5 $cmol_c$ dm^{-3} Ca, 0.4 $cmol_c$ dm^{-3} Mg, 6.5 $cmol_c$ dm^{-3} Al, and 56.7 $cmol_c$ dm^{-3} cation-exchange capacity.

Doses of limestone used for pH correction were determined following the incubation method proposed by Dunn (1943), by adding increasing doses of limestone to four soil samples moistened with distilled water. pH measurements were made using a glass electrode saturated with KCl and calibrated at pH 4.0 and 7.0 with standard buffer solutions. Final pH values in water were plotted against limestone doses, and the data were fitted by polynomial regression models to estimate the amount of limestone needed to reach pH 5.0 (low fertility) and 6.0 (high fertility). This procedure indicated that 7.6 and 19.0 g of dolomitic limestone should be added per experimental unit to achieve low and high soil fertility, respectively.

Fertility correction followed the recommendations of the Soil Chemistry and Fertility Commission (2016). For high fertility treatments, fertilizer doses were calculated to obtain a grain yield of 6,000 kg ha^{-1}. For low fertility treatments, triple superphosphate doses were determined as the ratio of the amount of phosphorus required to obtain 36 mg P dm^{-3} in soil (high availability) to the amount required to obtain 6 mg P dm^{-3} (low availability). Application of potassium chloride was not necessary, given that the level of potassium in soil was low.

Thus, low fertility treatments received the application of 7.6 g of dolomitic limestone and 1 g of triple superphosphate, which were incorporated into soil to raise the pH to 5.0 and maintain phosphorus and potassium levels low. High fertility pots were treated with 3.4 g of triple superphosphate, 2.4 g of potassium chloride, and 19 g of dolomitic limestone, raising the pH to 6.0. Limestone application was performed about 30 days before the initiation of the experiment, whereas fertilizers were applied on the day of sowing.

The experiment was installed on November 14, 2021. Soybean seeds were planted, five per pot, into pots filled with sifted soil. Seeds were previously treated with 2 mL kg^{-1} cyantraniliprole + thiamethoxam (Fortenza Duo®) and 3 mL kg^{-1} inoculant (Masterfix L). After reaching the V1 stage, plants were thinned to one per pot. Soil moisture was maintained close to field capacity by daily irrigation throughout the experimental period.

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

Leaf area was determined by measuring the length and width of the central leaflet of each trifoliolate leaf and applying the equation described by Richter et al. (2014): $LA = \alpha \times (w \times l)$, where LA is the leaf area (cm^2), l is the leaf length (cm), w is the largest width (cm), and α is an angular coefficient (2.0185). Two measurements of leaf area were performed, the first on the day of defoliation at R3 and the second at R5 (beginning of pod filling). The difference in leaf area between R3 and R5 was also determined.

Harvest was performed on April 9, 2018. After harvest, the following parameters were determined: number of pods per plant, number of grains per pod, thousand grain weight, grain yield per plant, biological yield, and harvest index. Number of pods per plant was determined by counting, considering pods that had at least one formed grain. Number of grains per pod was estimated by counting grains in 10 pods per plant selected at random, considering normal grains to be of small size and spherical shape. Thousand grain weight was estimated as the ratio of weight to number of grains per plant and adjusted to 13% moisture. Grain yield per plant was determined as grain weight per plant adjusted to 13% moisture.

Stems and pods were dried separately in a forced-air oven at 65°C until constant weight. After manual threshing of pods, biological yield was calculated as the sum of the dry weights of the stem, pods, and grains of each plant. Harvest index was obtained by dividing the dry grain weight of each plant by its biological yield.

Data were subjected to the *F*-test for analysis of variance at a level of significance of $p < 0.05$. In case of significance, means of the qualitative factor (soil fertility) were compared by Tukey's test and means of the quantitative factor (defoliation level) by polynomial regression, both at $p < 0.05$. The best-fitting model (whether linear or quadratic) was determined by evaluating the coefficient of determination.

RESULTS AND DISCUSSION

Table 1 shows the F- and p-values for the variables assessed in the experiment.

Table 1. Analysis of variance (*F*-values) for leaf area before defoliation at the R3 stage (LA_{R3}), leaf area at R5 (LA_{R5}), leaf area development between R3 and R5 ($LA_{R3–R5}$), grain yield per plant (GY_{plant}), thousand grain weight (TGW), number of pods per plant (NP_{plant}), number of grains per pod (NG_{pod}), biological yield (BY), and harvest index (HI) of soybean plants according to soil fertility (high and low) and defoliation level (0, 17, 33, 50, and 67%).

Source of variation	df	LA_{R3}	LA_{R5}	$LA_{R3–R5}$	GY_{plant}	TGW	NP_{plant}	NG_{pod}	BY	HI
Soil fertility (SF)	1	10.8**	22.8**	61.7**	158.4**	2.6^{ns}	48.2**	2.6^{ns}	109.7**	12.5**
Defoliation (D)	4	1.4^{ns}	21.4**	0.4^{ns}	9.1**	3.1*	7.0**	1.1^{ns}	6.3**	1.2^{ns}
SF × D	4	0.8^{ns}	0.6^{ns}	3.0*	1.2^{ns}	1.1^{ns}	3.0*	2.5^{ns}	0.6^{ns}	1.0^{ns}
Blocks	2	1.9^{ns}	2.8^{ns}	0.2^{ns}	1.9^{ns}	0.2^{ns}	3.4^{ns}	2.3^{ns}	15.3**	1.8^{ns}
Residuals	18									
Total	29									

* Significant at $p < 0.05$.
** Significant at $p < 0.01$.
ns, not significant ($p > 0.05$).

Table 2 presents the results of leaf area at R3 before defoliation. The parameter was influenced by soil fertility, being higher in plants grown in high fertility soil (Tables 1 and 2).

Table 2. Leaf area per plant at the R3 (beginning of pod formation) and R5 (beginning of pod filling) stages, grain yield per plant, biological yield, and harvest index of soybean as a function of soil fertility. Lages, Santa Catarina, Brazil, 2021/22.

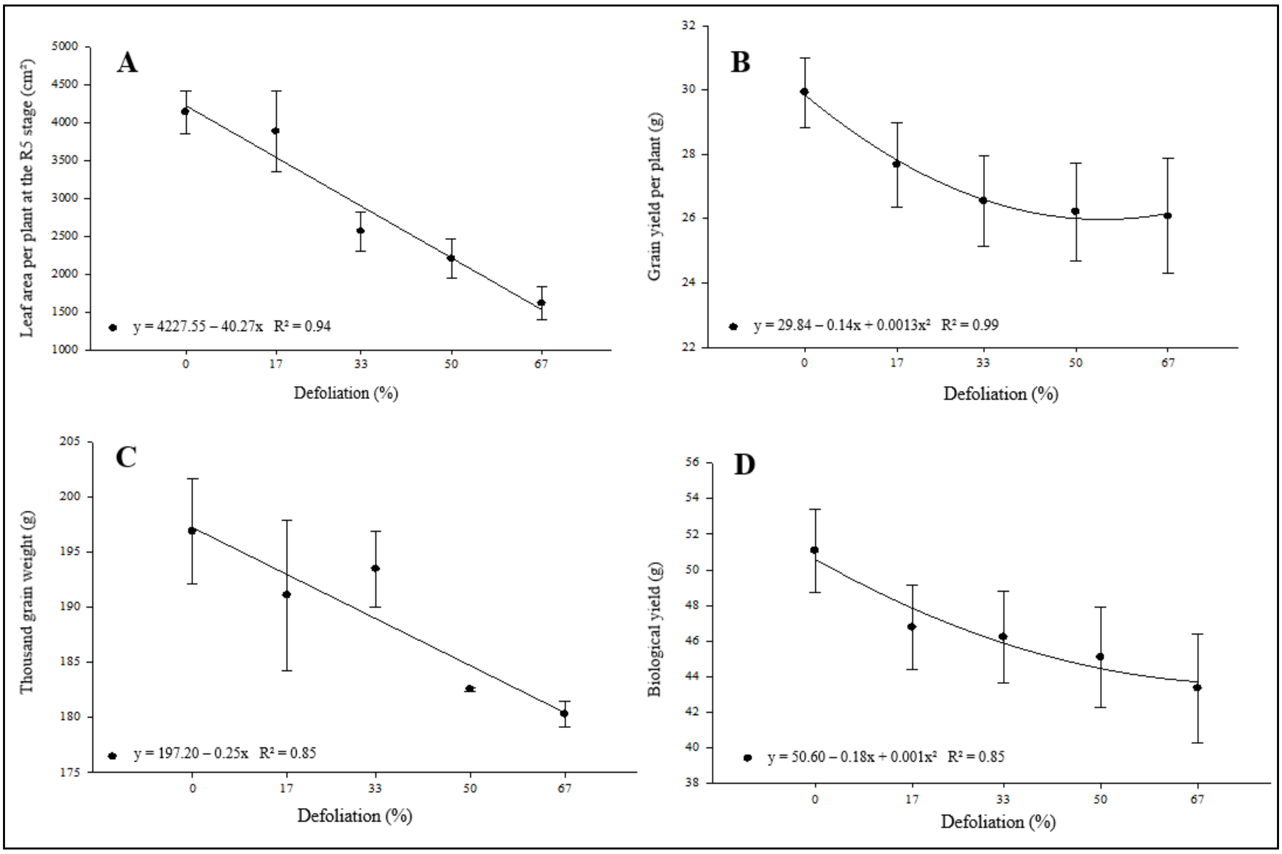
Item[1]	Soil fertility		CV (%)
	High	Low	
Leaf area at R3 (cm^2)[2]	$4,025^{a}$	$3,142^{b}$	20.5
Leaf area at R5 (cm^2)	$3,386^{a}$	$2,378^{b}$	20.0
Grain yield per plant (g)	30.3^{a}	24.3^{b}	11.3
Biological yield (g)	51.8^{a}	41.1^{b}	11.3
Harvest yield ($g\ g^{-1}$)	0.55^{b}	0.56^{a}	3.7

[1] Values are the mean of five defoliation levels (0, 17, 33, 50, and 67%).
[2] Leaf area before the application of defoliation treatments at R3.
[a,b] Means withing rows followed by different lowercase letters differ significantly at $p < 0.05$ by Tukey's test.
CV, coefficient of variation.

Similar findings were reported by Santos et al. (2014) and Rakocevic et al. (2022), who observed an increase in leaf area in plants under high-dose phosphorus treatment compared with low-dose phosphorus treatment, even when other nutrients were supplied to meet crop requirements.

In addition to being integral constituents of the photosynthetic apparatus, nutrients constitute plant leaves; they are necessary for the formation of leaf biomass. Thus, nutrient deficiency leads to a reduction in photosynthesis, leaf area index, and leaf area duration, limiting the time leaves can provide photoassimilates to sinks (Engels et al., 2012; Mu and Chen, 2021). Leaf area at R5 was influenced by soil fertility and defoliation level (Table 1). The parameter was higher in plants grown in high fertility soil, following the same trend observed before defoliation (Table 2). Leaf area depends on the environmental conditions of development phases. Stressors such as low temperature, soil salinity, water deficit, and nutrient deficiency reduce leaf area, although the magnitude of such a response depends on plant genotype (Engels et al., 2012; Shrestha et al., 2022).

Leaf area at R5 decreased linearly with increasing defoliation percentage, as estimated by considering the mean of both fertility levels (Figure 2A). There was a reduction of 402.7 cm^2 for every 10% of leaf area removed, resulting in a maximum leaf area loss of 63.8% at the highest level of defoliation compared with the control.

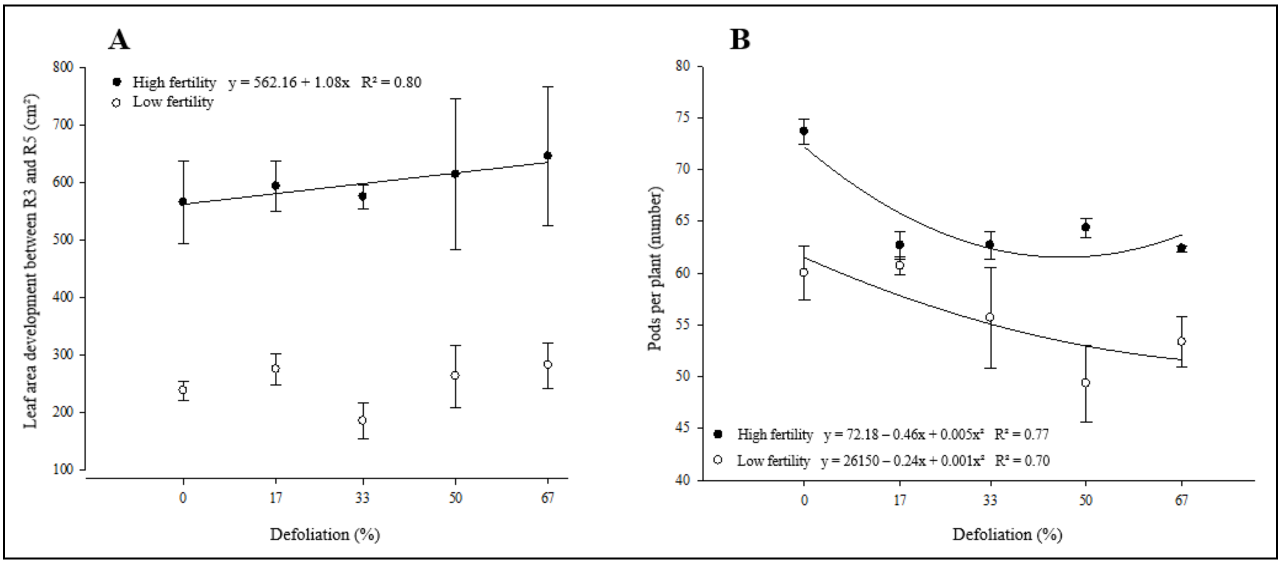


Values are the mean of two soil fertilization levels (high and low). Error bars represent standard errors.

Figure 2. (A) Leaf area per plant at the R5 stage (beginning of pod filling), (B) grain yield per plant, (C) thousand grain weight, and (D) biological yield of soybean as a function of defoliation treatments applied at the R3 stage. Lages, Santa Catarina, Brazil, 2021/22.

Durli et al. (2020) reported similar results when evaluating leaf area at R5 after defoliation at R3. The authors found that leaf area reduction was directly proportional to defoliation level, regardless of the maturation group of cultivars.

Leaf area development between R3 and R5 was influenced by the interaction between soil fertility and defoliation level (Table 1). Leaf area development was higher in plants grown in high fertility soil at all levels of defoliation (Figure 3A): leaf expansion increased linearly with defoliation percentage, by 10.8 cm^2 for every 10% of leaf area removed, representing an increase in leaf area of 12.9% at the highest level of defoliation as compared with the control. In the low-fertility environment, there was no significant change in leaf area with increasing defoliation.



Results are presented as mean and standard error (bars).

Figure 3. (A) Leaf area development between R3 (beginning of pod formation) and R5 (beginning of pod filling) stages and (B) number of pods per plant in soybean as a function of soil fertility and defoliation treatments applied at R3. Lages, Santa Catarina, Brazil, 2021/22.

The results demonstrate that foliar expansion after defoliation is greater when plants are grown in high fertility soil. Durli et al. (2020) observed an increase in leaf expansion as defoliation increased, suggesting that defoliation stimulates plants to relocate photoassimilates for the growth of new leaves as a strategy to compensate for leaf area losses.

Grain yield per plant was influenced by the main effects of soil fertility and defoliation (Table 1). Grain production was 24.7% higher in high fertility soil according to the mean values for the five levels of defoliation (Table 2). Improvement in productive performance resulting from good soil fertility conditions has been reported in previous studies. Gonçalves Júnior et al. (2010) found that grain yield increased proportionally to phosphorus and potassium availability in soil with medium and low concentrations of these nutrients, respectively. Carvalho et al. (2012) and Vonk et al. (2024) found that grain yield increased with mineral fertilization in soil with medium potassium levels and very low phosphorus contents. Similarly, Duarte et al. (2016) reported that grain yield per plant increased linearly with the increase in phosphate and potassium fertilization, which ranged from 0 to 400% of the recommended dose.

In a study conducted by Bender et al. (2015), it was found that soil fertilization significantly enhanced the accumulation of nutrients that were applied (N, P, K, S, and Zn) or not (Ca, Mg, Mn, B, and Cu). Thus, high nutrient availability favored absorption, stimulated total biomass production, and increased grain yield. Nutrient availability influences grain yield directly, in the case that nutrients are needed for a specific metabolic step, or indirectly, by altering the concentrations of photosynthates or phytohormones (Engels et al., 2012).

Grain yield per plant decreased quadratically with the increase in defoliation percentage (Figure 2B). There was a reduction of 3.5 g in grain yield per plant at the highest defoliation level (as estimated by using the mean of the two fertility levels). Such a value represents a decrease of 11.9% compared with the control. Similarly, Durli et al. (2020), observed a quadratic reduction in grain yield with an increase in defoliation level up to 66.6%, regardless of maturation group. However, the largest reduction occurred at a defoliation level of 16.6%. By contrast, Zuffo et al. (2015) and Schardong et al. (2025a, 2025b) found that grain yield was only reduced by high defoliation levels (66-99%) from R1 to R6.

The findings demonstrate that soybean is sensitive to soil fertility (Table 2) and loss of leaf area, given that a low defoliation level (17%) caused a reduction in grain yield per plant (Figure 2B). However, there were no significant interaction effects of soil fertility and defoliation on productive performance; the effects were independent and additive. Thus, our initial hypothesis, that the tolerance of soybean to defoliation is low in low fertility soils, was not confirmed.

The increase in leaf area between R3 and R5 in plants grown in high fertility soil did not result in higher grain yield compared with plants grown in low fertility soil (Figure 3A). In line with our results, Santos et al. (2015) reported that high leaf area index and dry matter did not result in higher grain yield in beans under the recommended fertilization scheme.

In a study conducted with four soybean cultivars, Müller et al. (2017) evaluated the effect of solar radiation interception by different canopy strata on grain yield. The authors observed that soybean 'NA 5909 RG' had the highest leaf area index and number of infertile nodes in the lower third canopy as a result of shading and low solar radiation interception. Thus, it was concluded that soybean yield depends in large part on the radiation intercepted by the lower part of the canopy. The lower canopy can account for up to 25% of the total grain yield, depending on the genotype.

In the current study, we observed higher leaf area and leaf area development (between R3 and R5) in plants grown in high fertility soil. It is possible to infer that such an increase in leaf area enhanced shading over lower canopy layers, limiting total photoassimilate synthesis. As a result, the expected advantage in grain production resulting from high fertility treatment, as compared with low fertility treatment, in the face of defoliation was not observed.

Thousand grain weight was influenced by defoliation (Table 1), decreasing linearly with increasing defoliation percentage (Figure 2C). There was a reduction of 2.5 g in grain weight for every 10% of leaf area removed. At the highest level of defoliation, the grain weight was 16.7 g lower than in the control, representing a decrease of 8.5%, as measured by the mean of fertility treatments. Durli et al. (2020) obtained similar findings. The authors reported that thousand grain weight decreased linearly with increasing defoliation up to 66.6%, regardless of maturation group. Zuffo et al. (2015) observed that only high levels of defoliation (66 and 99%) reduced grain weight at R3, R4, and R5 and Schardong et al. (2025a, 2025b) observed that only high levels of defoliation (66 and 99%) reduced grain weight at R2 and R5. Similarly, in the study of Glier et al. (2015), thousand grain weight was only reduced at 100% defoliation, even during the reproductive phase.

Thousand grain weight was not influenced by soil fertility, different from the expected. Theoretically, a small leaf area should result in the formation of lower weight grains in plants grown in low fertility soil. In agreement with our results, Gonçalves Júnior et al. (2010) observed no effect of increased phosphorus and potassium doses on grain weight in plants grown in soil with medium and low nutrient levels, respectively. Duarte et al. (2016) also did not observe a significant influence of phosphate or potassium fertilization (0 to 400% of the recommended dose) on grain weight. These results reinforce the importance of genotype characteristics for performance stability in plants under different environmental conditions.

Number of pods per plant was influenced by the interaction between soil fertility and defoliation (Table 1). The variable was higher in plants grown in high fertility soil, regardless of defoliation level, contributing to the higher grain yield per plant observed under this nutrient condition (Figure 3B, Table 2). Similar to the present study, previous reports observed an increase in pod number with the increase in soil fertility. Gonçalves Júnior et al. (2010) found that the number of pods per plant increased proportionally to phosphorus and potassium fertilization rate in soil with medium and low levels of these nutrients, respectively. Carvalho et al. (2012) also found that pod number increased as a function of mineral fertilization in soil with medium potassium and very low phosphorus contents. It is known that well-nourished plants exhibit greater photosynthetic activity and produce more photoassimilates, thereby minimizing flower abortion and enhancing pod number at harvest (Zanon et al., 2018).

Number of pods per plant decreased quadratically with increasing defoliation percentage in both soil fertility treatments (Figure 3B). There was a reduction of 8.4 and 9.8 pods per plant at the highest defoliation level, representing a decrease of 11.6 and 15.9% in plants grown in high and low fertility soil, respectively. Such behavior was also observed by Zuffo et al. (2015), who reported a reduction in number of pods per plant at all levels of defoliation (33, 66, and 99%) and stages of development (R1 to R6). Similarly, Durli et al. (2020) observed linear and quadratic reductions in number of pods per plant in soybean ‘NA 5909 RG’ and ‘TMG 7262 RR’, respectively, with defoliation levels of up to 66.6% at R3. Losses in leaf area negatively influence yield components by decreasing photoassimilate production (Damasceno et al., 2019). Thus, plants may abort pods and maintain those that can translocate photoassimilates from the remaining leaves (Silva et al., 2015).

Number of grains per pod ranged from 2.4 to 2.6 and was not influenced by soil fertility or defoliation (data not shown). This result corroborates those of Gonçalves Júnior et al. (2010) and Carvalho et al. (2012), who also did not observe significant effects of mineral fertilization on the number of grains per pod of soybean plants grown in soils with low phosphorus and potassium contents. This yield component had the lowest influence on grain yield, given that the number of grains per pod is characteristically little influenced by cultivation medium (Silva et al., 2015).

Biological yield was influenced by the main effects of soil fertility and defoliation (Table 1). Total phytomass was higher in soybean grown in high fertility soil (Table 2). In line with this finding, Bender et al. (2015) reported an increase in soybean biomass with the increase in nutrient availability. The authors compared two contrasting cultivation conditions, no fertilization and fertilization to achieve a yield of 5,000 kg ha^{-1}.

Biological yield decreased quadratically with increasing defoliation percentage (Figure 2D). There was a 15% reduction in biological yield at the highest level of defoliation, as compared with the control. Such a trend was also observed by Durli et al. (2020), who reported a reduction in biological yield with increased defoliation at R3 in three cultivars of different maturation groups. Schardong et al. (2025a, 2025b) also observe reduction in biological yield at the highest level of defoliation (66 and 100%). Stress or injury caused by defoliating agents can influence both the rate and duration of dry mass accumulation in plants (Taiz et al., 2017). Defoliation affects dry mass accumulation in soybean by reducing the effective leaf area for solar radiation interception and carbon fixation, resulting in lower biological yield via source reduction.

The harvest index was influenced by soil fertility (Table 1), being lower in plants grown under high fertility conditions (Table 2). Similar results were reported by Bender et al. (2015), who found that fertilized plants exhibited reduced harvest index, indicating that greater nutrient accumulation does not necessarily translate into increased assimilate allocation to grains. This is because sink capacity is determined by the number of sink organs (grains), storage cells per organ (endosperm cells per grain), and storage organelles per cell (amyloplasts per endosperm cell) (Engels et al., 2012). Therefore, a higher harvest index does not necessarily indicate higher absolute grain yield per plant, as also observed in the current study.

CONCLUSIONS

The soybean cultivar ‘NA 5909 RG’ demonstrated greater ability to recover from R3-stage defoliation when grown under high soil-fertility conditions. Regardless of defoliation intensity, plants grown in low-fertility soil produced lower grain yield per plant compared with those grown in high-fertility soil. Defoliation levels of **67% or**

higher significantly reduced grain yield per plant in both fertility conditions.

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REFERENCES

Bender, R., Haegele, J., Below, F., 2015. *Nutrient uptake, partitioning, and remobilization in modern soybean varieties.* Agronomy Journal, 107(2): 563-573. https://doi.org/10.2134/agronj14.0435

Boiça Júnior, A.L., Souza, B.H.S. de, Ribeiro, Z.A., Moraes, R.F.O. de, Eduardo, W.I., Nogueira, L., 2015. *A defesa das plantas ao ataque dos insetos*. In: Busoli, A.C., Castilho, R. de C., Andrade, D.J. de, Rossi, G.D., Viana, D. de L., Fraga, D.F., Souza, L.A. de. (eds.), Tópicos em entomologia agrícola. Maria de Lourdes Brandel-ME, Jaboticabal: 161-179.

Bortolotto, O.C., Pomari-Fernandes, A., Bueno, R.C.O. de F., Bueno, A. de F., Cruz, Y.K. da, 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. https://doi.org/10.33158/ASB.2015v1i1p25

Briske, D.D., and Richards, J.H., 1995. *Plant responses to defoliation: A physiological, morphological, and demographic evaluation*. In: Bedunah, D.J., Sosebee, R.E. (eds.), Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver: 635-710.

Carvalho, E., Rezende, P., Passos, A., Oliveira, J., 2012. *Diagnose foliar e produtividade da soja, em razão de doses e tecnologias de manufatura de fertilizantes formulados NPK.* Revista Brasileira de Ciências Agrárias, 7(3): 402-408. https://doi.org/10.5039/agraria.v7i3a1308

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*. Sociedade Brasileira de Ciência do Solo, Porto Alegre: 376.

Damasceno, L.J., Silva, V.F.A., Silva, J.N.D., Silva, P.A., Lima, C.C., Silva, J.P.D., Galvão, J.R., Melo, N.C., Valente, G.F., 2019. *Defoliation levels supported in soybean crop with no harm on productivity in the municipality of Parauapebas.* Journal of Agricultural Science, 11(17): 227-234. https://doi.org/10.5539/jas.v11n17p227

Duarte, T., Cruz, S., Soares, G., Sena Júnior, D., Machado, C., 2016. *Spatial arrangements and fertilizer doses on soybean yield and its components.* Revista Brasileira de Engenharia Agrícola e Ambiental, 20(11): 960-964. https://doi.org/10.1590/1807-1929/agriambi.v20n11p960-964

Dunn, L.E., 1943. *Lime requirement determination of soils by means of titration curves.* Soil Science, 56(5): 341-351. https://journals.lww.com/soilsci/Citation/1943/11000/Lime_Requirement_Determination_of_Soils_By_Means.3.aspx.

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): 402-411. https://doi.org/10.1590/1983-21252020v33n213rc

Engels, C., Kirkby, E., White, P., 2012. *Mineral nutrition, yield and source-sink relationships.* In: Marschner, P. (eds.), Marschner's mineral nutrition of higher plants. Academic Press, Oxford: 85-133.

Fehr, W.R., and Caviness, C.E., 1977. *Stages of soybean development.* Iowa State University of Science and Technology, Ames: 11.

Gonçalves Júnior, A., Nacke, H., Marengoni, N., Carvalho, E., Coelho, G., 2010. *Produtividade e componentes de produção da soja adubada com diferentes doses de fósforo, potássio e zinco*. Ciência e Agrotecnologia, 34(3): 660-666. https://doi.org/10.1590/S1413-70542010000300019

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

Hajibarat, Z., and Saidi, A., 2022. *Senescence-associated proteins and nitrogen remobilization in grain filling under drought stress condition.* Journal of Genetic Engineering and Biotechnology, 20(1): 101. https://doi.org/10.1186/s43141-022-00378-5

Hoffmann-Campo, C.B., Corrêa-Ferreira, B.S., Moscardi, F., 2012. *Soja: manejo integrado de pragas e outros artrópodes-praga.* Empresa Brasileira de Pesquisa Agropecuária, Brasília: 859.

Leolato, L.S., Sangoi, L., Souza, C.A., Kuneski, H.F., Scherer, R.L., Oliveira, V.L., Martins Junior, M.C., Kandler, R., 2022. *Soybean tolerance to defoliation at the vegetative and reproductive stages as a function of water restriction.* Acta Scientiarum, Agronomy, 44(1): e55639. https://doi.org/10.4025/actasciagron.v44i1.55639

Leolato, L.S., Sangoi, L., Martins Junior, M.C., Oliveira, V.L., Durli, M.M., Souza, C.A., 2023. *Sowing date influence on the soybean tolerance to* *defoliation at the beginning of pod formation.* Revista Ceres, 70(1): 78-86. https://doi.org/10.1590/0034-737X202370010009

Mu, X., and Chen, Y., 2021. *The physiological response of photosynthesis to nitrogen deficiency.* Plant Physiology and Biochemistry, 158: 76-82. https://doi.org/10.1016/j.plaphy.2020.11.019

Müller, M., Rakocevic, M., Caverzan, A., Chavarria, G., 2017. *Grain yield differences of soybean cultivars due to solar radiation interception.* American Journal of Plant Sciences, 8(11): 2795-2810. https://doi.org/10.4236/ajps.2017.811189

Poudel, S., Magar, L.P., Khatri, D., Pandit, M., Chiluwal, A., 2025. *Identifying the most sensitive growth stages of soybean to defoliation.* Scientific Reports, 15: 28268. https://doi.org/10.1038/s41598-025-12590-7

Rakocevic, M., Marchiori, P.E.R., Zambrosi, F.C.B., Machado, E.C., Maia, A.H.N., Ribeiro, R.V., 2022. *High phosphorus supply enhances leaf gas exchange and growth of young Arabica coffee plants under water deficit.* Experimental Agriculture, 58: e30. https://doi.org/10.1017/S0014479722000266

Richter, G.L., Zanon Júnior, A., Streck, N.A., Guedes, J.V.C., Kräulich, B., Rocha, T.S.M.D., Winck, J.E.M., 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. https://doi.org/10.1590/1678-4499.0179

Rogers, C.W., Adams, C.B., Marshall, J.M., Hatzenbuehler, P., Thurgood, G., Dari, B., Loomis, G., Tarkalson, D.D., 2024. *Barley residue biomass, nutrient content, and relationships with grain yield.* Crop Science, 64(4): 2345-2367. http://dx.doi.org/10.1002/csc2.21263

Santos, V., Cardoso, D., Ferreira, E., Silva, Á., Sousa, D., 2014. *Ação de bioestimulantes no desempenho do cultivo de soja em duas condições de adubação fosfatada.* Revista Verde de Agroecologia e Desenvolvimento Sustentável, 10(3): 01. https://doi.org/10.18378/rvads.v10i3.3323

Santos, L.A., Soratto, R.P., Fernandes, A., Gonsales, J.R., 2015. *Crescimento, índices fisiológicos e produtividade de cultivares de feijoeiro sob diferentes níveis de adubação.* Revista Ceres, 62(1): 107-116. https://doi.org/10.1590/0034-737X201562010014

Schardong, I.S., Reisig, D.D., Vann, R., Huseth, A., Guedes, J.V.C., 2025a. *Does defoliation affect late planted soybean yield?* Crop Protection, 197: 107352. https://doi.org/10.1016/j.cropro.2025.107352

Schardong, I.S., Reisig, D.D., Vann, R., Huseth, A., 2025b. *Artificial defoliation effects on full season and double crop soybean yields.* Crop Protection, 197: 107347. https://doi.org/10.1016/j.cropro.2025.107347

Shrestha, S.L., Sams, C., Allen, F., 2022. *Genotypic Variation for Salt Tolerance within and between 'Alamo' and 'Kanlow' Switchgrass (Panicum virgatum L.) Cultivars.* Agronomy, 12(4): 973. https://doi.org/10.3390/agronomy12040973

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

Taiz, L., Zeiger, E., Møller, I.M., Murphy, A., 2017. *Fisiologia vegetal.* Artmed, Porto Alegre: 858.

Vonk, J., Nafziger, E., Fontes, G.P., 2024. *Soybean response to nitrogen fertilizer in different soils.* Crop, Forage and Turfgrass Management, 10(2): e20304 https://doi.org/10.1002/cft2.20304

Yang, J., and Zhang, J., 2023. *Simultaneously improving grain yield and water and nutrient use efficiencies by enhancing the harvest index in rice.* Crop and Environment, 2: 157-164. https://doi.org/10.1016/j.crope.2023.07.001

Zanon, A.J., Silva, M.R. da., Tagliapetra, E.L., Cera, J.C., Bexaira, K.P., Richter, G.L., Duarte Junior, A.J., Rocha, T.S.M. da., Weber, P.S., Streck, N.A., 2018. *Ecofisiologia da soja: visando altas produtividades.* Santa Maria: 136.

Zuffo, A.M., Zambiazzi, E.V., Gesteira, G.S., Rezende, P.M., Bruzi, A.T., Soares, I.O., Gwinner, R., 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. https://doi.org/10.5897/AJAR2014.9369