Defoliation tolerance of soybean cultivars commercially released in different decades

Tolerancia a la defoliación de cultivares de soya liberados para su comercialización en diferentes décadas

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ABSTRACT

Breeding programs have increased the precocity and yield potential of modern soybean cultivars. Such changes may have altered the crop tolerance to defoliation due to the smaller leaf area of modern cultivars. The objective of this study was to determine the tolerance to defoliation of soybean cultivars commercialized in Brazil in different decades, their photosynthetic efficiency and the relationship between photosynthetic efficiency and tolerance to defoliation in the reproductive phase. The experiment was set in a greenhouse with controlled humidity and temperature, in the municipality of Lages, Santa Catarina State, South of Brazil, during the growing season of 2018/2019. A randomized block design was used, with treatments arranged in a 5×5 factorial scheme. The first factor was composed of five soybean cultivars released in different years: Davis (1968), Paraná (1974), BR-16 (1985), FT Abyara (1991), and Brasmax Elite IPRO (2014). The second factor consisted of five levels of defoliation applied in stage R3: 0, 16.6, 33.3, 50.0, and 66.6%. Leaf area, photosynthetic activity parameters, grain yield and its components were determined. Brasmax Elite IPRO had the lowest grain yield per plant and did not increase yield compared to older cultivars, regardless of defoliation level. There were no significant differences in photosynthetic efficiency or defoliation tolerance between the modern cultivar Brasmax Elite IPRO and the old cultivars Davis, Paraná, BR-16, and FT Abyara.

Key words: *Glycine max* L. Merrill, leaf area, grain yield, photosynthetic activity.

RESUMEN

Los programas de mejoramiento han aumentado la precocidad y el potencial de rendimiento de los cultivares de soya modernos. Dichos cambios pueden haber alterado la tolerancia del cultivo a la defoliación, siendo la pérdida de área foliar un factor agravante de la pérdida de productividad. El objetivo de este estudio fue determinar la tolerancia a la defoliación de cultivares de soya comercializados en Brasil en diferentes décadas, su eficiencia fotosintética y la relación entre la eficiencia fotosintética y la tolerancia a la defoliación en la fase reproductiva. El experimento se realizó en un invernadero con humedad y temperatura controladas, en el municipio de Lages en el estado de Santa Catarina, Sur de Brasil, en la temporada de crecimiento 2018/2019. Se utilizó un diseño de bloques al azar, con tratamientos en esquema factorial 5×5. El primer factor estuvo compuesto por cinco cultivares de soya comercializados en diferentes años: Davis (1968), Paraná (1974), BR-16 (1985), FT Abyara (1991) y Brasmax Elite IPRO (2014). El segundo factor consistió en cinco niveles de defoliación aplicados en la etapa R3: 0, 16.6, 33.3, 50.0 y 66.6%. Se determinó área foliar, parámetros de actividad fotosintética, rendimiento de grano y sus componentes. Brasmax Elite IPRO mostró el rendimiento de grano más bajo por planta y no aumentó el rendimiento en comparación con los cultivares más antiguos, independientemente del nivel de defoliación. No hubo diferencias significativas en la eficiencia fotosintética ni en la tolerancia a la defoliación entre el cultivar moderno Brasmax Elite IPRO y los antiguos cultivares Davis, Paraná, BR-16 y FT Abyara.

Palabras clave: *Glycine max* L. Merrill, área foliar, rendimiento de grano, actividad fotosintética.

Introduction

Over the past five decades, plant-breeding programs have developed soybean cultivars with desirable agronomic traits and high adaptability to different field conditions. Experimental studies are necessary to determine the best cultivar for a given production region, searching for genotypes that best fulfill a series of requirements, such as resistance to insect defoliation, suitable plant architecture to maximize light absorption, and resistance/tolerance to pathogens (Zanon *et al.*, 2018).

The leaf mesophyll is the most active photosynthetic tissue in higher plants. It is responsible for the interception of solar

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radiation and the assimilation of atmospheric CO_2 , transforming light energy into chemical energy (Taiz *et al.*, 2017). Leaf area loss is one of the main factors affecting soybean yield. The maximum yield of soybean is determined by the plant's ability to intercept solar radiation and accumulate dry mass during the vegetative and reproductive stages (Heiffig *et al.*, 2006; Koester *et al.*, 2014). Although the productive potential of soybean has increased in recent years, leaf area loss is still one of the main problems studied by researchers around the world. Breeders try to develop cultivars better adapted to this condition, entomologists aim to select genotypes capable of resisting the attack of defoliating pests, and physiologists search to identify plant materials that are increasingly efficient in converting light energy into biomass (Lopes & Lima, 2015).

The reproductive phase is the most decisive time for soybean yield. This stage encompasses four periods of plant development: flowering, pod formation, grain filling, and maturation (Neumaier *et al.*, 2018). Stressful events during the reproductive phase may lead to low yields. Defoliating insects, such as *Anticarsia gemmatalis* and *Chrysodeixis includens*, can significantly reduce crop yield if defoliation surpasses 15% after the beginning of flowering (Moscardi *et al.*, 2012; Glier *et al.*, 2015).

In Brazil, soybean crop yield increased from 1,140 kg ha⁻¹ in the 1970s to 3,333 kg ha⁻¹ in 2017/2018 (EMBRAPA, 2018). This increase is attributed to the development of new cultivars, whose yields have increased by 34 kg ha⁻¹ per year (Balbinot Junior *et al.*, 2017). Toledo *et al.* (1990) reported genetic gains of 1.8% in early-cycle cultivars and 1.3% in semi-early cultivars in the State of Paraná, Brazil. Alliprandini *et al.* (1993) observed annual yield gains of 6.62, 4.54, and 0.89% in early, semi-early, and mediumcycle cultivars, respectively. Despite these advances in crop productivity, few studies have explored how physiological characteristics have contributed to the increase in grain yield of soybean cultivars released in different decades. Furthermore, the relationships between photosynthetic efficiency, defoliation tolerance, and grain yield in old and modern soybean cultivars still need to be determined.

This study was conducted based on the following hypotheses: the modern cultivar Brasmax Elite is more productive than the old cultivars because of its higher photosynthetic efficiency; the modern cultivar Brasmax Elite is more sensitive to defoliation than the old cultivars due to its smaller leaf area and greater productive potential; and the yield gain promoted by soybean breeding is greater when leaf area is preserved.

The main objectives of the experiment were to determine the impact of leaf area loss on grain yield of soybean cultivars commercially released in different decades, compare the photosynthetic efficiency of these genotypes, and assess the relationship of photosynthetic efficiency with defoliation tolerance during the reproductive phase.

Materials and methods

A greenhouse experiment was conducted in Lages, Santa Catarina, Brazil, during the 2018/2019 growing season. The geographical coordinates of the site are 27°48'58" S; 50°19'34" W. The experimental design was a randomized block with three replicates. Treatments were arranged in a 5×5 factorial design. The experiment had 75 experimental units $(5 \times 5 \times 3)$. The plants were cultivated in 5 L PVC pots, with soil-based substrate from a commercial soybean cultivation environment with the following characteristics: 405 g kg⁻¹ of clay; pH (water) 5.1; 24.9 mg dm⁻³ of P, 223 mg dm⁻³ of K; 3.7 g kg⁻¹ of organic matter; 4.7 cmolc dm⁻³ of Ca; 1.9 cmolc dm⁻³ of Mg; 1.0 cmolc dm⁻³ of Al and 20.9 cmolc dm⁻³ CEC, arranged over three benches (each with 25 experimental units) in an environment kept at 25±10°C and 70% relative air humidity. The first factor comprised five soybean cultivars commercially released in different decades: Davis (1968), Paraná (1974), BR-16 (1985), FT Abyara (1991), and Brasmax Elite IPRO (2014) (Tab. 1). These cultivars were selected for their relevance

Cultivar	Year of release	Maturity group	Growth habit	Technology
Davis	1968	7.0	Determined	Conventional
Paraná	1974	6.5	Determined	Conventional
BR-16	1985	6.5	Determined	Conventional
FT Abyara	1991	8.0	Determined	Conventional
Brasmax Elite	2014	5.5	Undetermined	IPRO

TABLE 1. Characteristics of soybean cultivars used in the study.

IPRO: Technology that confers resistance to the herbicide glyphosate and control and/or suppression of caterpillars.

in cultivated area during the 1960s, 1970s, 1980s, 1990s, and the current century.

The second factor comprised five defoliation levels: 0 (control), 16.6, 33.3, 50.0, and 66.6%. According to Moscardi *et al.* (2012), defoliation levels of 16.6 and 33.3% are close to the threshold of economic damage for soybean in the reproductive (15%) and vegetative (30%) phases, respectively. Defoliation treatments were applied at the R3 stage (beginning of pod formation) and assessed according to the phenological scale proposed by Ritchie *et al.* (1977). Defoliation was performed manually with scissors. The leaves were cut longitudinally until reaching the desired level of defoliation in all plants simultaneously, regardless of growth habit, as shown in Figure 1.

Disease control was performed with 1.5 ml L⁻¹ of difenoconazole + cyproconazole (Cypress[®]), 1 g L⁻¹ of azoxystrobin + benzovindiflupyr (Elatus[®]), 2.6 ml L⁻¹ of trifloxystrobin + prothioconazole (Fox[®]). Fungicides were applied at the growth stages of V8, R1, and R5, respectively. Pest control was performed with 0.5 ml L⁻¹ of λ -cyhalothrin + chlorantraniliprole (Ampligo[®]) and 1 ml L⁻¹ of thiamethoxam + λ -cyhalothrin (Engeo Pleno[®]). Insecticides were applied on plants at the stages of V8, R1. To correct the soil used in the pots, 310 kg ha⁻¹ of triple superphosphate and 155 kg ha⁻¹ of potassium chloride were used.

Leaf area was determined at the R3 (beginning of pod formation) and R5 (beginning of grain filling) stages and used to calculate leaf expansion. The length and largest width of the central leaflet of each trifoliate leaf was measured in all plants. Leaf area was calculated by the following equation proposed by Ritcher *et al.* (2014):

$$LA = L \times W \times \alpha \tag{1}$$

where LA is the leaf area (cm²), *L* is the leaf length (cm), *W* is the leaf width (cm), and α is the angular coefficient for soybean crops (2.0185).



FIGURE 1. Representative images of soybean leaves at different defoliation levels.

Turek, Martins Junior, Sangoi, Kandler, Oliveira, Kuneski, Coelho, Tirelli, and Márquez: Defoliation tolerance of soybean cultivars commercially released in different decades Gas exchange in leaves was determined at the R5 stage. Measurements were performed between 9:00 and 11:00 h at the apex of the central leaflet of completely expanded leaves using an open-system, portable photosynthesis meter (IRGA LI-6400XT, LI-COR). Gas exchange values were used to determine net carbon assimilation rate (A), transpiration rate (E), and stomatal conductance (g_s).

Grain harvest was carried out manually on April 1, 2019, using hand pruners. The filled pods were oven-dried at 35°C for 4 d. Dried samples were used to determine the number of pods per plant, number of grains per pod, number of grains per plant, thousand-grain weight, and grain yield (adjusted to 13% moisture).

Statistical analysis

Experimental data were subjected to analysis of variance by the *F*-test. When statistical significance was detected, comparisons of mean values between cultivars (qualitative factor) were performed by Tukey's test and differences between defoliation levels (quantitative factor) were assessed by regression analysis. The level of significance was set at P<0.05. Analyses were performed using the SISVAR software (Ferreira, 2003).

Results and discussion

Leaf area at R3 (before defoliation), leaf area at R5 (after defoliation at R3), and leaf expansion (between R3 and R5) were influenced by the main effect of the cultivar (Tab. 2). Davis had the highest leaf area at the R3 stage, followed by FT Abyara and BR-16. Paraná and Brasmax Elite had the smallest leaf areas at the beginning of pod formation (Tab. 3).

TABLE 3. Leaf area at R3 (LA-R3, before defoliation), leaf area at R5 (LA-R5, after application of defoliation treatments at R3), leaf expansion (LE, from R3 to R5) in soybean cultivars subjected to different defoliation levels. Lages, Santa Catarina, Brazil, 2018/2019.

Cultivar	LA-R3 (m²)	LA-R5 (m²)	LE (m²)
Davis	0.88ª	0.93ª	0.04 ^b
Paraná	0.41°	0.59°	0.18ª
BR-16	0.60 ^b	0.66 ^{bc}	0.06 ^b
FT Abyara	0.71 ^b	0.73 ^b	0.03 ^b
Brasmax Elite	0.39°	0.45 ^d	0.06 ^b
CV(%)	20.10	18.37	61.05

CV - coefficient of variation.

* Values are the means of five defoliation treatments. Means within columns followed by the same lowercase letters are not significantly different at P<0.05 according to Tukey's test.

The leaf area at R5 also differed significantly among cultivars. Similar to the results for the R3 stage, Davis and Brasmax Elite had the highest and lowest leaf areas, respectively, at R5. Paraná had the highest leaf expansion, as shown by the mean value of the five defoliation treatments. Brasmax Elite had the smallest leaf area before and after defoliation.

Brasmax Elite belongs to the maturity group 5.5, the lowest among the genotypes used in the experiment (Tab. 1), explaining why it had the smallest leaf area at R3. The lower the maturity group of a soybean cultivar, the earlier it blooms, and the smaller its leaf area at the end of flowering (Zanon *et al.*, 2018). The time from emergence to R1 was 44, 49, 50, 51, and 56 d for Brasmax Elite, Paraná, BR-16, 'FT Abyara', and Davis, respectively.

Since Brasmax Elite was the only cultivar with indeterminate growth habit (Tab. 1), it was supposed to have a greater ability to expand new leaves between R3 and R5,

TABLE 2. *F*-values according to the analysis of variance for leaf area at R3 (LA-R3, before defoliation), leaf area at R5 (LA-R5, after application of defoliation treatments at R3), leaf expansion (LE, from R3 to R5), net assimilation rate (*A*), transpiration rate (*E*), and stomatal conductance (g_s) in soybean cultivars subjected to different defoliation levels. Lages, Santa Catarina, Brazil, 2018/2019.

Source of variation	df	LA-R3	LA-R5	LE	A	E	g s
Blocks	2	2.64 ^{ns}	2.87 ^{ns}	0.35 ^{ns}	1.4 ^{ns}	0.7 ^{ns}	1.36 ^{ns}
Cultivars (C)	4	45.25 [*]	30.36*	27.66*	5.7*	18.2*	3.94*
Defoliation levels (D)	4	-	0.29 ^{ns}	0.86 ^{ns}	2.6 ^{ns}	1.3 ^{ns}	0.90 ^{ns}
$C \times D$	16	-	0.48 ^{ns}	0.78 ^{ns}	1.3 ^{ns}	0.6 ^{ns}	0.87 ^{ns}
Error	48						
Total	74						

df - degrees of freedom, * - significant at P<0.05, and ns - not significant.

which did not happen. This may be because Brasmax Elite exhibited very early maturity, reaching the end of the cycle at about 125 d, with a vegetative phase of 46 d after sowing. Compared with older cultivars, for which the vegetative stage ranged from 51 to 58 d after sowing, Brasmax Elite has a shorter cycle.

Net carbon assimilation, transpiration rate, and stomatal conductance at the beginning of grain filling were significantly influenced by the main effect of the cultivar (Tab. 2). The net carbon assimilation rate of Davis was lower than that of the other cultivars, which did not differ from each other (Tab. 4). The modern cultivar Brasmax Elite presented the highest values of transpiration rate and stomatal conductance, on the average of five defoliation levels.

TABLE 4. Net assimilation rate (*A*), transpiration rate (*E*), and stomatal conductance (g_s) of soybean cultivars at the R5 stage. Lages, Santa Catarina, Brazil, 2018/2019.

Cultivar	A (µmol CO ₂ m ⁻² s ⁻¹)	<i>E</i> (mmol H ₂ O m ⁻² s ⁻¹)	g_{s} (µmol CO ₂ m ⁻² s ⁻¹)
Davis	17.7 ^b	6.9 ^b	0.30 ^b
Paraná	22.2ª	9.7ª	0.34 ^{ab}
BR-16	22.1ª	6.1 ^b	0.31 ^b
FT Abyara	24.1ª	7.3 ^b	0.35 ^{ab}
Elite	22.5ª	9.9ª	0.39ª
CV(%)	17.8	17.3	19.41

CV - coefficient of variation, * - values are the means of five defoliation treatments. Means within columns followed by the same lowercase letters are not significantly different at P<0.05 according to Tukey's test.

One of the study's hypotheses was that Brasmax Elite is more productive than old cultivars because of its higher photosynthetic efficiency. The results described in Table 4 show that the modern cultivar had higher transpiration rate and stomatal conductance values. These physiological parameters are correlated with photosynthetic activity, as higher values indicate greater stomatal opening, which favors the flow of CO_2 from the atmosphere to chloroplasts (Koester *et al.*, 2014; Taiz *et al.*, 2017). However, such effects did not lead to a higher net carbon assimilation rate in the modern cultivar when compared with Paraná, BR-16, and FT Abyara.

Defoliation can reduce transpiration and photosynthesis. However, if the reduction in leaf area is not drastic, soybean plants may continue to perform photosynthesis at sufficient levels to ensure grain production (Moscardi *et al.*, 2012). In the present study, defoliation level had no significant effects on net carbon assimilation or stomatal conductance (Tab. 2). These findings suggest that defoliation of up to 66% did not compromise photosynthetic activity at the beginning of grain filling, regardless of the cultivar.

Grain yield per plant, number of pods per plant, number of grains per pod, number of grains per plant, thousand grain weight, and harvest index were influenced by the main effect of the cultivar (Tab. 5).

TABLE 5. *F*-values according to the analysis of variance for number of pods per plant (NP_{plant}), number of grains per pod (NG_{pod}), number of grains per plant (NG_{plant}), thousand grain weight (TGW), grain yield per plant (GY_{plant}), and harvest index (HI) of soybean cultivars subjected to different defoliation levels. Lages, Santa Catarina, Brazil, 2018/2019.

Source of variation	df	NP _{plant}	NG _{pod}	NG _{plant}	TGW	\mathbf{GY}_{plant}	HI
Blocks	2	0.2 ^{ns}	3.8*	0.5 ^{ns}	0.2 ^{ns}	0.1 ^{ns}	0.3 ^{ns}
Cultivars (C)	4	13.5*	4.8*	9.6*	23.3*	4.4*	4.7*
Defoliation levels (D)	4	0.2 ^{ns}	0.6 ^{ns}	0.5 ^{ns}	0.6 ^{ns}	1.6 ^{ns}	1.6 ^{ns}
$C\timesD$	16	0.6 ^{ns}	1.1 ^{ns}	0.5 ^{ns}	0.2 ^{ns}	0.6 ^{ns}	0.6 ^{ns}
Error	48						
Total	74						

df - degrees of freedom, *- significant at P<0.05, and ns-not significant (P>0.05).

FT Abyara had the highest number of pods per plant (n=118) and number of grains per pod (Tab. 6). As a result, it had the highest number of grains per plant. The number of grains per pod did not differ significantly among cultivars, with values ranging from 2.0 to 2.3. According to Mundstock and Thomas (2005), cropping conditions usually do not affect the number of grains per pod. The behavior of this yield component demonstrates the uniformity of genetic breeding, standardizing the parameter at approximately two grains per pod.

TABLE 6. Number of pods per plant (NP_{plant}), number of grains per pod (NG_{pod}), number of grains per plant (NG_{plant}), thousand grain weight (TGW), grain yield per plant (GY_{plant}), and harvest index (HI) of soybean cultivars subjected to different defoliation levels. Lages, Santa Catarina, Brazil, 2018/2019.

Cultivar		NGpod	NG _{plant}	TGW (g)	GY _{plant} (g)	HI
Davis	96 ^b	2.0 ^b	184 ^{bc}	183.7ª	33.2ª	49.0ª
Paraná	86 ^{bc}	2.3ª	179 ^{bc}	180.7ª	32.1 ^{ab}	46.5 ^{ab}
BR-16	102 ^{ab}	2.2 ^{ab}	207 ^{ab}	166.0 ^{ab}	34.1ª	49.7ª
FT Abyara	118ª	2.3ª	238ª	128.7°	30.6 ^{ab}	46.3 ^{ab}
Elite	79°	2.2 ^{ab}	165°	162.0 ^b	26.6 ^b	39.4 ^b
CV(%)	16.7	8.9	18.3	10.6	17.2	15.7

CV - coefficient of variation, * - values are the means of five defoliation treatments. Means within columns followed by the same lowercase letters are not significantly different at P<0.05 according to Tukey's test.

There was no significant effect of defoliation level on number of pods or grains per plant (Tab. 5). According to Zanon *et al.* (2018), these yield components have the highest impact on soybean yield. Souza *et al.* (2014) argued that defoliation level does not influence the total number of grains or grain yield in soybean when artificial defoliation occurs during vegetative stages. Peluzio *et al.* (2004) concluded that plants exhibit low pod numbers only when total defoliation is performed during pod formation or grain filling.

The thousand grain weight was lowest in FT Abyara, in agreement with the compensatory effect between grain number and grain weight, as reported by Mundstock and Thomas (2005) and Zanon *et al.* (2018). The cultivars with the highest thousand grain weights were Davis (183.8 g) and Paraná (180.8 g).

BR-16 and Davis had the highest grain yields and harvest indices, and Brasmax Elite the lowest (Tab. 6). Therefore, under the controlled conditions of the current study, the modern cultivar did not have a higher yield than the older cultivars. Such results disagree with those reported by Todeschini *et al.* (2019), who tested 29 soybean cultivars released between 1965 and 2011. In the referred study, modern cultivars showed higher yield, harvest index, and number of pods per plant than older cultivars. The behavior observed in the present study was contrary to the initial hypothesis that yields gains provided by genetic improvement programs are greater when leaf area is preserved. Regardless of the level of defoliation, Brasmax Elite produced fewer pods and grains per plant than cultivars released in the last century.

One factor that might have prevented Brasmax Elite from expressing its maximum productive potential is the cultivar's high nutritional requirement. Nearly $60 \text{ kg of } P_2 O_5$, $60 \text{ kg of } P_2 O_5$, 6kg of K₂O and 250 kg of N are required to produce 3000 kg ha⁻¹ of soybean grains (Oliveira et al., 2007). Contemporary soybean production is characterized by high technological levels (Balbinot Junior et al., 2017). Farmers must employ various resources to meet the nutritional requirements of modern cultivars, thereby increasing yields and profit margins. All cultivars used in the experiment received the same fertilizer amount. It is possible that the fertilization rates used in the trial were not sufficient to meet the demands of Brasmax Elite. Other factors that may help to explain the results are that the experiment was conducted in a greenhouse, and each experimental unit comprised only one plant. This experimental setup may not reflect what occurs in the field, where intraspecific competition is more pronounced, particularly in older cultivars, which belong to later maturity groups and have greater leaf areas (Barros et al., 2002).

The reduction in leaf area did not significantly affect yield or its components in any of the cultivars used in this study. Possibly, this behavior was due to the phenological stage when the stress was imposed (R3). According to Parcianello et al. (2004), the most critical stage for losses in the photosynthetic area is the beginning of grain filling (R5), when yield loss is proportional to the increase in defoliation intensity. Gazzoni and Moscardi (1998) studied four levels of defoliation (0, 33, 67, and 100%) at four stages of development (V3, V8, R2, and R6) in the cultivar Paraná. Only defoliation levels above 67% affected grain production at the R6 stage. Other major agronomic characteristics, such as maturity date, lodging, and plant height, were not affected by levels. Ribeiro and Costa (2000) subjected BR 16 to different levels of defoliation (0, 17, 33, 50, 67, and 100%) at different development stages (V9, R3, R5, and R6). They found that yield decreased only in plants subjected to defoliation levels greater than 67%. Therefore, our results agree with Gazzoni and Moscardi (1998) and Ribeiro and Costa (2000), who evaluated two of the five cultivars used here.

Another factor that may explain why the defoliation level did not significantly influence the number of grains per plant was the fact that the experiment was set under greenhouse conditions, with experimental units consisting of one plant. In this environment, the amount of light received by leaves from the lower third of the stem is greater than that obtained under field conditions, where crop densities range from 200,000 to 400,000 plants ha⁻¹. Lower leaves may act as photoassimilate sinks in the field because they are shaded during the reproductive stage (Lopes & Lima, 2015). On the other hand, under greenhouse conditions, such leaves may act as sources of photoassimilates, as they receive high amounts of solar radiation. This change in source/sink ratio might have mitigated the negative effects of defoliation on grain production among cultivars.

Conclusions

Defoliation levels up to 66.6% applied at the R3 stage did not affect net carbon assimilation at R5 or the number of grains per plant of the evaluated soybean cultivars grown in a protected environment. There were no significant differences on the photosynthetic efficiency and sensibility to defoliation between the old cultivars Davis, Paraná, Br 16 and FT Abyara and the modern cultivar Elite. The cultivars with the highest mass of 1,000 grains were Davis and Paraná, with 183.8 g and 180.8 g, respectively. The modern cultivar Brasmax Elite did not show increased yield compared with older cultivars, regardless of defoliation level.

Conflict of interest statement

The authors declare that there is no conflict of interests regarding the publication of this article.

Author's contributions

TLT and LS designed the experiments; TLT, MCMJr, HFK, RK, LAT, JFM, and VLO carried out the field and laboratory experiments; TLT, MCMJr, HFK, LS, AEC and RK contributed to the data analysis; LS, TLT, MCMJr, HFK, AEC, LAT, JFM, RK, and VLO wrote the article. All authors reviewed the final version of the manuscript.

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