

Original Article

Effects of previous infestation with *Bemisia tabaci* MEAM1 on the resistance to *Chrysodeixis includens* in Bt and non-Bt soybean plants

Efeito da infestação prévia com *Bemisia tabaci* MEAM1 na resistência a *Chrysodeixis includens* em plantas de soja Bt e não-Bt

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Abstract

Transgenic Bt soybean plants have been developed to control insect pests, such as *Anticarsia gemmatilis* and *Chrysodeixis includens*. This objective has been achieved successfully; however, recently, some authors claimed that Bt soybean plants have been more susceptible than non-Bt soybean to *Bemisia tabaci* MEAM1. In addition, it is unknown whether Bt soybean plants infested by *B. tabaci* become less resistant to target pests. Therefore, this study aimed to evaluate: (i) whether the previous infestation with *B. tabaci* can compromise Bt and non-Bt soybean resistance to *C. includens*; (ii) the effects of *B. tabaci* infestations on Bt and non-Bt soybean plant growth; and (iii) whether *B. tabaci* feeding reduces contents of chlorophyll and carotenoids of soybean plants. Bt and non-Bt soybean plants pre-infested with *B. tabaci* showed no changes in resistance to *C. includens*. Bt soybean plants infested with *B. tabaci* showed a lower plant height than uninfested plants. Differently, non-Bt soybean plants exhibited no reduction in plant growth due to *B. tabaci* feeding. Bt soybean plants suffered a reduction in dry matter only under double infestation (*B. tabaci* and *C. includens*), while non-Bt soybean plants experienced reduction in dry matter when infested with *B. tabaci* and *C. includens* or by *C. includens* only. *B. tabaci* feeding did not alter contents of chlorophyll and carotenoids, and perhaps the reduction in plant growth was related to salivary toxins. Concluding, both Bt and non-Bt soybean plants were susceptible to *B. tabaci* feeding, evidencing necessity of developing soybean cultivars resistant to *B. tabaci*.

Keywords: chewing insects, genetically modified organisms, plant resistance, plant-insect interaction, sap-sucking insects.

Resumo

A soja Bt (transgênica) foi desenvolvida para controlar insetos-praga como *Anticarsia gemmatilis* e *Chrysodeixis includens*. Este objetivo foi alcançado com sucesso; no entanto, recentemente, alguns autores afirmaram que as plantas de soja Bt têm sido mais suscetíveis do que a soja não-Bt a *Bemisia tabaci* MEAM1. Além disso, não se sabe se plantas de soja Bt infestadas por *B. tabaci* tornam-se menos resistentes às pragas-alvo. Portanto, este estudo teve como objetivo avaliar: (i) se a infestação prévia de *B. tabaci* pode comprometer a resistência da soja Bt e não Bt a *C. includens*; (ii) os efeitos de infestações de *B. tabaci* no crescimento de plantas de soja Bt e não Bt; e (iii) se a alimentação de *B. tabaci* reduz os teores de clorofila e carotenoides das plantas de soja. Plantas de soja Bt e não Bt pré-infestadas com *B. tabaci* não apresentaram alterações na resistência a *C. includens*. Plantas de soja Bt infestadas com *B. tabaci* apresentaram menor altura de planta do que plantas não infestadas. Diferentemente, as plantas de soja não-Bt não apresentaram redução no crescimento das plantas devido à alimentação de *B. tabaci*. Plantas de soja Bt sofreram redução de matéria seca apenas sob infestação dupla (*B. tabaci* e *C. includens*), enquanto plantas de soja não Bt apresentaram redução de matéria seca quando infestadas por *B. tabaci* e *C. includens* ou apenas por *C. includens*. A alimentação de *B. tabaci* não alterou os teores de clorofila e carotenoides, e talvez a redução no crescimento da planta esteja relacionada a toxinas salivares. Concluindo, tanto as plantas de soja Bt quanto as não-Bt foram suscetíveis à alimentação de *B. tabaci*, evidenciando a necessidade do desenvolvimento de cultivares de soja resistentes a *B. tabaci*.

Palavras-chave: insetos mastigadores, organismos geneticamente modificados, resistência de plantas, interação inseto-planta, insetos sugadores.

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1. Introduction

In Brazil, the cultivation of plants that express toxins from *Bacillus thuringiensis* (Bt) started in 2005, when the Brazilian National Technical Commission on Biosafety (CTNBio), linked to the Ministry of Science and Technology (MCT), approved the commercial release of that technology to control insects. Cotton (*Gossypium hirsutum* L. [Malvales: Malvaceae]) was the first Bt plant commercialized in Brazil, expressing only one Bt protein in the plant tissue (CTNBio, 2007, 2008). *B. thuringiensis* is a gram-positive soil bacterium that produces protein crystals, the delta-endotoxins, which exhibit lethal action on some species of insect pests from the orders: Lepidoptera, Coleoptera, and Diptera. Nearly 50 different Bt families were discovered and classified according to their action in the insect groups (Carneiro et al., 2009).

The most known Bt proteins are the crystal proteins, commonly referred as to *Cry*, which control immatures of some insect orders. Over the last few decades, due to biotechnology advances, many of the Bt genes responsible for the expression of insecticidal proteins have been introgressed into species of crop plants, such as maize (*Zea mays* L.) (Cyperales: Poaceae), soybeans [*Glycine max* (L.) Merr.] (Fabales: Fabaceae), and cotton (Arends et al., 2021).

Soybeans with Bt technology target larvae of *Anticarsia gemmatalis* Hübner, 1818 (Lepidoptera: Erebiidae), *Chrysodeixis includens* (Walker, 1858) (Lepidoptera: Noctuidae), *Chloridea virescens* (Fabricius, 1777) (Lepidoptera: Noctuidae), *Crociosema aporema* (Walsingham, 1914) (Lepidoptera: Tortricidae), *Elasmopalpus lignosellus* (Zeller, 1848) (Lepidoptera: Pyralidae), and *Helicoverpa zea* (Boddie, 1850) (Lepidoptera: Noctuidae) (Blanco et al., 2016). It is noteworthy that the first two species are the main soybean defoliators. However, Bt soybean does not control other soybean pests such as stink bugs, leaf beetles (Coleoptera: Chrysomelidae), *Bemisia tabaci* (Gennadius, 1889) (Hemiptera: Aleyrodidae) MEAM1 (Middle East Minor-Asia Minor 1, formerly referred to as biotype B) (Fernandes et al., 2022), and mites (Roggia et al., 2016). *B. tabaci* in high infestation produces an excrement deposit on the lower leaves. This is a rich sugar-excrement that, when exposed to the sun and to high temperature, favors the growth of *Capnodium* sp., a fungus known as fumagina. Soybean yield losses caused by *B. tabaci* feeding injury are related with the abundant formation of fumagina on the plant leaves. Fumagina excess increases leaf ethylene content, inducing an early leaf senescence. This early leaf fall may impair plant development and grain yield, depending on its intensity (Moscardi et al., 2012; Oliveira et al., 2021).

In this context, Almeida et al. (2021) reported that several Bt soybean fields showed more severe damage caused by feeding of *B. tabaci* than non-Bt soybean fields. In the laboratory, the authors observed that Bt soybean provided better conditions for *B. tabaci* reproduction than non-Bt soybean. Therefore, the current study aimed to evaluate resistance of a Bt and a non-Bt (conventional) cultivar to *B. tabaci* MEAM1 and *C. includens*. It was also investigated if the previous feeding of *B. tabaci* MEAM1 cause a reduction in soybean resistance to *C. includens*,

because we noted a severe plant dry matter reduction due to the pest sucking. This evaluation was also supported by the fact that activation of the phytohormones jasmonic acid (JA) and salicylic acid (AS) depends on the insect feeding habit. The JA pathway is activated especially in response to chewing-biting herbivores and cell-content feeders (e.g., mites). Differently, the SA pathway is triggered if the plant is injured by piercing-sucking insects (Schweiger et al., 2014). However, it is worth noting that antagonism between the JA and SA pathways depends especially on the plant species (Caarls et al., 2015; Ullah et al., 2022). In addition, it was evaluated if Bt and non-Bt soybean cultivars show a significant reduction in chlorophyll and carotenoid contents after the pest attack.

2. Materials and Methods

The experiments were carried out in Dourados, State of Mato Grosso do Sul, Brazil, using a completely randomized design, under a factorial scheme 2×3 [two soybean cultivars and three infestation treatments (plants infested by *B. tabaci* MEAM1 and *C. includens*, plants infested with only *C. includens*, and uninfested plants)]. Thus, six treatments were assessed: (i) Bt soybean infested with *B. tabaci* and *C. includens*; (ii) Bt soybean infested with *C. includens* only; (iii) non-Bt soybean infested with *B. tabaci* and *C. includens*; (iv) non-Bt soybean infested with *C. includens* only; (v) uninfested Bt soybean; and (vi) uninfested non-Bt soybean. The Bt soybean cultivar was BRS 1061 IPRO, which expresses the gene *Cry1Ac*, and the non-Bt soybean cultivar was BRS 539, both developed by Embrapa.

2.1. Resistance in *Bemisia tabaci*-infested Bt and non-Bt soybean cultivars to *Chrysodeixis includens*

Soybean plants were grown in a greenhouse of the School of Agricultural Sciences (FCA; Faculdade de Ciências Agrárias) of Universidade Federal da Grande Dourados (UFGD), which has an exhaust fan and a pad-fan cooling system used to maintain internal temperature at 28 °C, under a luminosity regime of 14:10 (light:dark) and natural relative humidity. Six soybean seeds were sown per replicate (10 replicates per treatment) in 7-plastic pots filled with a substrate constituted by three parts of soil (Dystroferric Red Latosol) and one part of organic compost (Plante Verde, Guarapuava, PR, Brazil). Plants were thinned to two plants per replicate (plastic pot) 2 weeks after sowing. Each pair of plants was covered using a voile bag, supported by three bamboo stakes and tied with a string at the superior part of each pot, and irrigated when necessary. Thirteen days after plant emergence, a group of plants was infested with 100 *B. tabaci* adults. Eighteen days later, plant height and number of leaves were assessed by comparing *B. tabaci*-infested with uninfested plants, aiming to determine soybean tolerance in Bt and non-Bt plants.

At 34 days after plant emergence, all plants (except control) were infested with two *C. includens* neonates, which were handled using a soft-bristle paintbrush. Seven days after enclosing *C. includens*, larval mortality (%) was recorded and weight (mg) was obtained with the aid of a precision analytical scale (model 2204, Bioscale, China).

After finishing the experiment, infested and non-infested plants were cut at the soil surface level using scissors, placed in paper bags, and then dried at ambient temperature ($25 \pm 1^\circ\text{C}$) for 24 hours. Subsequently, the plants were dried at 60°C for 48 hours in an oven (Odontobrás, model EL 1.4; Ribeirão Preto, SP, Brazil). Thereafter, the plants were weighed using a precision analytical scale.

2.2. Chemical analysis

Contents of chlorophyll *a*, *b*, total ($\mu\text{g cm}^2$) and carotenoids ($\mu\text{g cm}^2$) were quantified from a fully expanded leaflet per plant. An amount of 1.0 g was weighed, and then macerated with pestle in mortar in 8.0 mL of 80% acetone, according to the methodology of Barbieri Junior et al. (2010). Next, the solutions were taken for centrifugation using a microcentrifuge (MCD-200, H. T.) at 1,500 rpm for 10 minutes. Then, absorbance reading was performed at the wavelengths of 470, 645, and 663 nm using a spectrophotometer (SP-220, Biospectro). The concentrations of chlorophylls and carotenoids were calculated according to the methodologies of Arnon (1949) and Lichtenthaler and Buschmann (2001), respectively. Four replicates were used to perform these analyses.

2.3. Statistical analysis

Data were checked for normality of residuals (Shapiro-Wilk) and homogeneity of variances (Levene) using the statistical software SAS (Version 9.0, SAS Institute, Cary, NC, USA). These data fit in the normality requirements and therefore were analyzed by one- or two-way ANOVA for the main effects of soybean cultivar, infestation treatment, and their interaction. When significant differences were found, means were compared using Tukey's test ($\alpha = 0.05$).

3. Results

3.1. Resistance in *Bemisia tabaci*-infested Bt and non-Bt soybean cultivars to *Chrysodeixis includens*

With respect to *C. includens* larval mortality, significant differences were observed for the variable 'soybean cultivar' (Bt \times non-Bt) ($F = 24.07$; $df = 1, 36$; $P < 0.0001$). A greater mortality was noted when *C. includens* larvae fed on leaves of Bt soybean plants compared with non-Bt plants (Figure 1). However, there were no significant differences when considering larval mortality within the factor 'infestation treatment' ($F = 1.67$; $df = 1, 36$; $P = 0.2049$) or for the interaction between soybean cultivar and infestation treatment ($F = 0.60$; $df = 1, 36$; $P = 0.4436$) (Figure 2).

Due to greater *C. includens* larval mortality when fed on the Bt soybean cultivar, larval weight was evaluated only for larvae fed on non-Bt soybean leaves. The previous infestation of non-Bt soybean plants with *B. tabaci* did not affect *C. includens* larval weight gain (1.6 ± 0.59 mg) compared with larvae fed on leaves of uninfested plants (2.18 ± 0.52 mg) ($F = 0.52$; $df = 1, 13$; $P = 0.4830$).

Bt soybean plants (cultivar BRS 1061 IPRO) infested with *B. tabaci* had a lower plant height than uninfested Bt soybean plants ($F = 9.54$; $df = 1, 18$; $P = 0.0063$) (Figure 3A).

In contrast, non-Bt soybean plants (cultivar BRS 539) did not exhibit reduction in plant height after *B. tabaci* infestation ($F = 0.06$; $df = 1, 18$; $P = 0.8076$) (Figure 3B).

There were no significant differences in total number of leaves considering Bt soybean infested (4.6 ± 0.18 leaves) or uninfested (4.9 ± 0.17 leaves) with *B. tabaci* ($F = 1.96$; $gl = 1, 18$; $P = 0.1785$). Similarly, no significant differences were found in the total number of leaves between *B. tabaci*-infested (6.1 ± 0.18 leaves) and uninfested (6.0 ± 0.16 leaves) non-Bt soybean plants ($F = 0.04$; $df = 1, 18$; $P = 0.8364$).

Lower dry matter was observed for double-infested (*B. tabaci* + *C. includens*) Bt soybean plants than for uninfested plants or those infested with *C. includens* ($F = 6.79$; $gl = 2, 27$; $P = 0.0041$) (Figure 4A). In contrast, lower dry matter was recorded for double-infested non-Bt soybean plants compared with *C. includens*-infested or uninfested plants ($F = 16.53$; $gl = 2, 27$; $P < 0.0001$) (Figure 4B). Lower dry matter was also found in *C. includens*-infested non-Bt soybean plants compared with uninfested plants (Figure 4B).

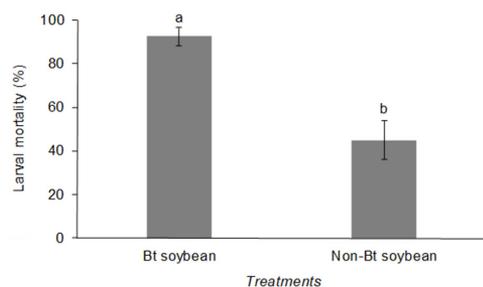


Figure 1. Larval mortality (mean \pm SE) of *Chrysodeixis includens* fed on Bt (cultivar BRS 1061 IPRO) or non-Bt (cultivar BRS 539) soybean plants.

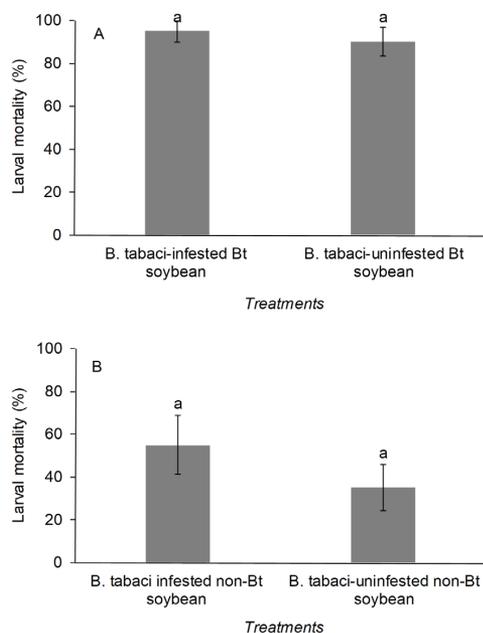


Figure 2. Larval mortality (mean \pm SE) of *Chrysodeixis includens* fed on *Bemisia tabaci*-infested or *B. tabaci* uninfested soybean plants (Bt [A] or non-Bt [B] soybean).

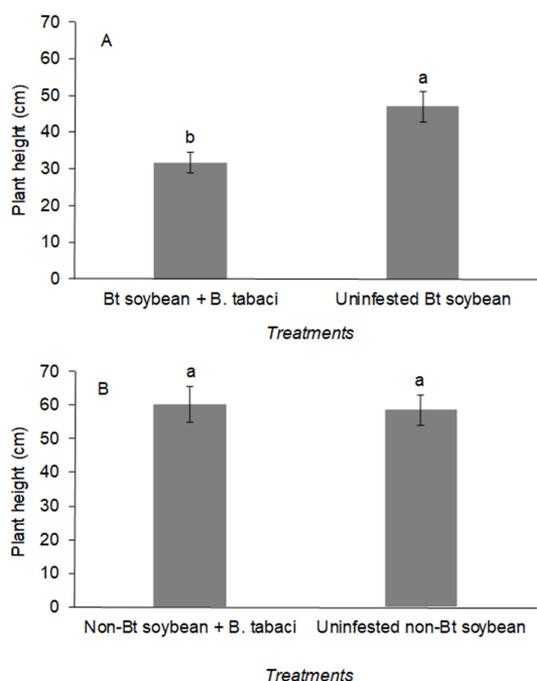


Figure 3. Plant height (mean \pm SE) of Bt (cultivar BRS 1061 IPRO) (A) and non-Bt (cultivar BRS 539) (B) soybean infested or uninfested with *Bemisia tabaci* MEAM1.

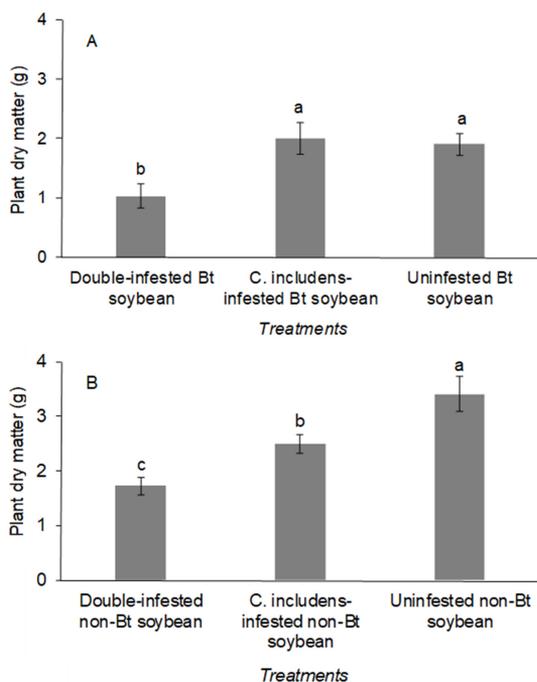


Figure 4. Plant dry matter (mean \pm SE) of Bt (A) or non-Bt (B) soybean plants under different infestation treatments.

3.2. Chemical analysis

No significant differences were noted in chlorophyll *a* contents, with respect to Bt and non-Bt soybean cultivars

($F = 4.37$; $df = 1, 12$; $P = 0.0585$) (Bt soybean = $19.56 \pm 0.52 \mu\text{g cm}^2$; non-Bt soybean = $20.70 \pm 0.23 \mu\text{g cm}^2$), infestation treatment ($F = 1.65$; $df = 1, 12$; $P = 0.2227$), or the interaction between soybean cultivars and infestation treatment ($F = 1.28$; $df = 1, 12$; $P = 0.2796$).

Significant differences were not found in chlorophyll *b* contents, considering Bt and non-Bt soybean cultivars ($F = 0.77$; $df = 1, 12$; $P = 0.3967$) (Bt soybean = $12.77 \pm 1.90 \mu\text{g cm}^2$; non-Bt soybean = $14.21 \pm 2.75 \mu\text{g cm}^2$), infestation treatment ($F = 2.40$; $df = 1, 12$; $P = 0.1473$), or the interaction between soybean cultivars and infestation treatment ($F = 0.04$; $df = 1, 12$; $P = 0.8382$).

No significant differences were registered for carotenoids contents, with respect to Bt and non-Bt soybean cultivars ($F = 0.87$; $df = 1, 12$; $P = 0.3688$) (Bt soybean = $2.94 \pm 0.05 \mu\text{g cm}^2$; non-Bt soybean = $3.32 \pm 0.07 \mu\text{g cm}^2$), infestation treatment ($F = 1.59$; $df = 1, 12$; $P = 0.2317$), or for the interaction between soybean cultivars and infestation treatment ($F = 0.05$; $df = 1, 12$; $P = 0.8278$).

Concerning the total chlorophyll content, there were no effects of Bt and non-Bt soybean cultivars ($F = 1.87$; $df = 1, 12$; $P = 0.1963$) (Bt soybean = $32.33 \pm 2.55 \mu\text{g cm}^2$; non-Bt soybean = $34.92 \pm 3.01 \mu\text{g cm}^2$), infestation treatment ($F = 2.95$; $df = 1, 12$; $P = 0.1114$), or their interaction ($F = 0.26$; $df = 1, 12$; $P = 0.6200$).

4. Discussion

Almeida et al. (2021) reported that a Bt soybean cultivar (M8330IPRO) favored *B. tabaci* reproduction compared with a non-Bt cultivar (M8866). The current study confirmed the damaging effects of *B. tabaci* on another Bt soybean (BRS 1061 IPRO), due to reduced plant height and dry matter. However, despite the great damages experienced by Bt soybean plants infested by *B. tabaci*, their resistance to *C. includens* was unchanged, which can be observed in the percentage of *C. includens* larval mortality.

Pre-infestation of Bt and non-Bt soybean plants by *B. tabaci* did not induce greater susceptibility to *C. includens*. This was a valid hypothesis because *B. tabaci* feeding commonly activates the salicylic acid (SA) defensive pathway in plants (which is also activated by biotrophic plant pathogens), while suppressing the activation of the jasmonic acid (JA) pathway, known for interfering with chewing insects' development (Prieto et al., 2021). This phenomenon, induced susceptibility, starts possibly due to a complex of effector proteins (or so called elicitors) that are injected into host plants by the insect (Chen, 2007). Probably, *B. tabaci* did not induce susceptibility to *C. includens* in Bt soybean plants because Cry toxins are not governed by JA pathway. Concerning the non-Bt soybean, *C. includens* did not exhibit a better development on *B. tabaci*-infested plants because perhaps these sucking-insects are not able to induce susceptibility to that non-Bt soybean cultivar.

The non-Bt soybean plants had no reduction in plant height as a result of *B. tabaci* infestation. However, at the end of the experiment, non-Bt soybean plants showed a greater reduction in plant dry matter when infested

by *B. tabaci* and *C. includens* than *C. includens*-infested or uninfested plants. The fact that both Bt and non-Bt soybean plants displayed susceptibility to *B. tabaci*, indicates that it is necessary to evaluate soybean germplasm for resistance to this pest. For example, Baldin et al. (2017) assessed several soybean genotypes for antixenosis to *B. tabaci*, a resistance category in which a plant is not suitable for feeding or oviposition of an arthropod pest (Smith, 2005). The authors found that the genotypes 'IAC-17,' 'IAC-19,' 'Jackson,' 'P98Y11,' PI-229358, TMG1176 RR, and UX-2569-159 showed antixenosis to *B. tabaci*, and, therefore, may be exploited in soybean breeding programs for resistance to the pest. Cruz and Baldin (2017) evaluated antibiosis in soybean genotypes to *B. tabaci*, a resistance category in which the plant exerts adverse effects on insect biology (Smith, 2005), such as longer development period and higher mortality. The authors reported moderate levels of antibiosis, with the genotypes 'P98Y11' and 'TMG132 RR' extending the development cycle, and UX-2569-159 causing high nymphal mortality. Cruz et al. (2016) evaluated soybean tolerance to *B. tabaci* and noted that the genotype 'KS-4202' showed no yield losses after pest feeding. Thus, these results suggest that there is germoplasm available for use in plant breeding aiming to develop soybean resistant to *B. tabaci*.

Bemisia tabaci, as a sap-sucking insect, can remove chlorophyll from plants during feeding, which can compromise plant tolerance (Jindal et al., 2009). However, in the current study, no significant differences were found in chlorophyll contents between *B. tabaci*-infested and uninfested plants. Nevertheless, *B. tabaci*-infested plants showed a significant reduction in dry matter compared with uninfested plants. This lower dry matter may be a consequence of salivary toxins injected into plants by *B. tabaci* during feeding (Ragab, 2013).

Bt soybean plants have exerted efficient control of different species of caterpillars, such as *Anticarsia gemmatilis* Hübner (Lepidoptera: Erebidae) and *C. includens* (Conte et al., 2020). However, according to Almeida et al. (2021) and the findings of the current study, it is necessary to incorporate resistance to *B. tabaci* in modern soybean cultivars. Efforts have been made by plant breeders to improve soybean resistance to another sap-sucking insect, *Aphis glycines* Matsumura (Hemiptera: Aphididae), by incorporating *Rag* genes into commercial cultivars (O'Neal et al., 2018). This indicates that plant breeding is perhaps an interesting tactic to enhance soybean resistance to *B. tabaci*.

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