Survival and development of *Spodoptera eridania*, *Spodoptera cosmioides* and *Spodoptera albula* (Lepidoptera: Noctuidae) on genetically-modified soybean expressing Cry1Ac and Cry1F proteins

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Abstract

BACKGROUND: *Spodoptera eridania* (Stoll), *S. cosmioides* (Walker) and *S. albula* (Walker) (Lepidoptera: Noctuidae) are considered secondary pests of soybean in South America. The genetically-modified soybean DAS-444Ø6-6 × DAS-81419-2 with tolerance to 2,4-dichlorophenoxyacetic acid (2,4-D), glyphosate and ammonium glufosinate herbicides (event DAS-444Ø6-6) and insect-resistance due to expression of Cry1Ac and Cry1F Bt proteins (event DAS-81419-2) may provide a potential tool for integrated pest management (IPM) of these species in soybean fields. Based on this, we conducted bioassays to evaluate the survival and development of *S. eridania*, *S. cosmioides* and *S. albula* fed on Cry1Ac/Cry1F-soybean leaf tissue.

RESULTS: *Spodoptera eridania* and *S. cosmioides* fed on Cry1Ac/Cry1F-soybean showed longer developmental time, lower larval and egg to adult survival compared to those fed on non-Bt soybean, reducing the population growth of these species. *Spodoptera albula* also had lower larval survival and number of insects that reached adulthood on Cry1Ac/Cry1F-soybean. However, no significant effects of Cry1Ac/Cry1F-soybean on population growth parameters were detected in this species.

CONCLUSIONS: Soybean with stacked events DAS-444Ø6-6 × DAS-81419-2 expressing Cry1Ac/Cry1F Bt proteins provide population suppression of *S. eridania* and *S. cosmioides*. However, this Bt soybean had minimal effects on *S. albula*, and is unlikely to have negative population-level effects on this species. It is expected that under field conditions, other control tactics must be integrated with Cry1Ac/Cry1F-soybean for the management of these *Spodoptera* species.

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Keywords: transgenic soybean; secondary pest species; life history traits; integrated pest management

1 INTRODUCTION

Soybean, *Glycine max* (L.) Merrill (Fabaceae: Phaseoleae), is the most important agricultural crop in Brazil, Argentina, Paraguay and Uruguay, being cultivated on approximately 59 million ha per season (35 million ha in Brazil).1 3 The main soybean Lepidopteran pests are velvetbean caterpillar, *Anticarsia gemmatalis* (Hübner), soybean looper, *Chrysodeixis includens* (Walker), Old World bollworm, *Helicoverpa armigera* (Hübner), and tobacco budworm, *Chloridea virescens* (F.).3 6 However, outbreaks of *Spodoptera* species have been reported in soybean fields, including *S. frugiperda* (Smith), *S. eridania* (Stoll), *S. cosmioides* (Walker) and *S. albula* (Walker).7 9 Of these species, *S. frugiperda* is an emerging soybean pest due to increased infestations and damage observed on

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soybean in recent seasons in Brazil. *Spodoptera eridania* is the most important *Spodoptera* pest species on soybean in the Cerrado region, and southern Brazil.\(^9,10\) In contrast, *S. cosmioides* and *S. albula* occur at relatively lower frequencies.\(^9\) However, *S. cosmioides* can consume almost twice the soybean leaf area as other species from this genus.\(^11\)

*Spodoptera* species are considered secondary soybean pests in South American countries.\(^7,8\) However, sporadic infestations of these species can cause significant yield loss to soybean due to their defoliation capacity\(^1\) and damage to reproductive structures (flowers and pods).\(^9,12\) Outbreaks of *Spodoptera* species in Brazilian soybean fields may be influenced by the widespread deployment of transgenic soybean plants expressing *Bacillus thuringiensis* Berliner (Bt) proteins.\(^13\) Transgenic Cry1Ac-soybeans provide effective control of key defoliating pests (A. *gemmatalis*, *C. includens*, *C. virescens* and *H. armigera*), but only minimal activity against *Spodoptera* species.\(^13\) The Bt soybeans with sustained efficacy against primary pests can create opportunities for secondary pests to become more prevalent. Outbreaks of these species may also be associated with the crop production landscape, such as cropping systems where there is an overlap and/or succession of cultivated host plants across seasons that provides available food resources for their survival and development.\(^1,2,13\)

In 2018, Bt soybean was the main control tactic for management of lepidopteran pests in South America, representing 41% of the total soybean plantings in Brazil, Argentina, Paraguay and Uruguay.\(^2,19\) Recently, a new Bt soybean (event DAS-44406-6 × DAS-81419-2) was approved for commercialization in Brazil.\(^20\) The DAS-44406-6 event (Enlist E3®, Corteva Agriscience, Wilmington, DE, USA) expresses the enzymes 5-enolpyruvyl shikimate-3-phosphate synthase (2mEPSPS), phosphinothricin acetyltransferase (PAT), and aryloxyalkanoate dioxygenase 12 (AAD-12) that confer tolerance to the herbicides glyphosate, glufosinate ammonium, and 2,4-dichlorophenoxyacetic acid (2,4-D), respectively. The DAS-81419-2 event (Conkesta®, Corteva Agriscience) consists of insect-resistant technology that expresses Cry1Ac and Cry1F Bt proteins\(^20,21\) and PAT that confers tolerance to the herbicide glufosinate ammonium as a selectable marker. This Bt technology demonstrates efficacy against *A. gemmatalis*, *C. includens*, *C. virescens* and *H. armigera*,\(^22,23\) which are the main pest species for the development of Bt soybean events.

Transgenic plants expressing Cry1Ac and Cry1F Bt proteins have shown good activity against some *Spodoptera* species.\(^24\) Thus, understanding the survival and development of *Spodoptera* species on Cry1Ac/Cry1F-soybean technology is particularly important to support integrated pest management (IPM), insect resistance management (IRM) programs and best agricultural practices to manage these species in soybean fields. In this study, we present data from the first studies that evaluate the survival and development of *S. eridania*, *S. cosmioides* and *S. albula* on Bt soybeans expressing both Cry1AC and Cry1F proteins (event DAS-44406-6 × DAS-81419-2).

## 2 MATERIAL AND METHODS

### 2.1 Populations of *Spodoptera* species

Two populations of *S. eridania* and *S. cosmioides* and a single population of *S. albula* were collected in commercial plantings of non-Bt soybean (more than 200 larvae per species per location) in distinct soybean growing regions of Brazil (Table 1). After collection, larvae were taken to the laboratory and placed on an artificial diet consisting of white bean, wheat germ and yeast (adapted from Greene et al.),\(^27\) and maintained at 25 ± 2°C with a 14 h:10 h light/dark photoperiod. Neonates from the F1 generation of each species and population were used to perform these studies.

### 2.2 Soybean plants

Plants of Cry1Ac/Cry1F-soybean (event DAS-44406-6 × DAS-81419-2) and a non-Bt soybean isolate (experimental variety – maturity group 5.0) were cultivated in a greenhouse in 12-L plastic pots (four seeds/pot) containing two parts of soil and one part of composted plant material from January to March of 2019. Before the bioassays, Bt and non-Bt plants were checked for Bt protein expression using detection kits for Cry1Ac and Cry1F (Envirologix, São Paulo, SP, Brazil).

### 2.3 Biological parameters of *Spodoptera* species on Cry1Ac/Cry1F-soybean

Bioassays were performed with soybean leaves of Cry1Ac/Cry1F-soybean (event DAS-44406-6 × DAS-81419-2) and non-Bt soybean isolines from the R1 to R3 growth stages. Leaves were removed from the middle third and top of the plants and placed on a gelled mixture of agar–water at 2.5% in 50-mL plastic cups. Each cup was infested with a single neonate and then sealed and maintained in a room at 25 ± 2°C with a 14 h:10 h light/dark photoperiod. The experimental design was completely randomized with ten replicates of ten larvae, totaling 100 larvae/species/treatment. Leaves were replaced every 48 h. The following biological parameters were evaluated: duration and survival of egg, larva, pupa and total development (egg to adult); larval weight at 14 days; pupal weight 24 h after pupal formation and number of eggs per female. The number of eggs was assessed daily from 18 couples kept in polyvinyl chloride (PVC) cages (23-cm height × 10-cm diameter) internally coated with a paper towel and closed at the top with a voile-type fabric. To determine the embryonic period and survival, 50 to 100 eggs of the second oviposition position were obtained from each couple. The biological parameters of each *Spodoptera* species on Cry1Ac/Cry1F-soybean and non-Bt soybean isolines were compared by t-test (*P* < 0.05) using the PROC TTEST procedure in SAS® 9.1.28

### 2.4 Population growth parameters of *Spodoptera* species on Cry1Ac/Cry1F-soybean

To estimate parameters related to population growth potential, fertility life tables were estimated for *Spodoptera* species on Cry1Ac/Cry1F-soybean (event DAS-44406-6 × DAS-81419-2) and non-Bt soybean isolines. The mean length of a generation (*T*), the net reproductive rate (*R*₀ – average number of female offspring produced from a cohort of females), and the intrinsic rate of increase (*r*ₘ – rate of natural increase of a population) were estimated by the jackknife technique using ‘lifetable.sas’ protocol developed by Maia et al.\(^29\) in SAS® 9.1.28 This protocol calculates confidence intervals for all estimated parameters, and applies one-sided and two-sided t-tests to perform pairwise comparisons between groups (*P* ≤ 0.05).

## 3 RESULTS

### 3.1 Biological parameters of *Spodoptera* species on Cry1Ac/Cry1F-soybean

No significant differences in the duration and survival of egg and pupal stages of *S. eridania* and *S. cosmioides* populations fed Cry1Ac/Cry1F-soybean (event DAS-44406-6 × DAS-81419-2) and non-Bt soybean were detected (Fig. 1). However, larval
development was significantly longer for *S. eridania* and *S. cosmioides* on Cry1Ac/Cry1F-soybean (31 and 32 days, respectively) than on non-Bt (20 and 18 days, respectively). These species took 10 days longer for development into adults when feeding on Cry1Ac/Cry1F-soybean. Larval survival of *S. eridania* and *S. cosmioides* feeding on Cry1Ac/Cry1F-soybean (< 45% survival) was lower than those feeding on non-Bt soybean (> 70% survival). This significantly reduced the numbers of *S. eridania* and *S. cosmioides* that completed their life cycle on Cry1Ac/Cry1F-soybean (10 and 39% survival, respectively), compared with those on non-Bt soybean (31 and 65% survival, respectively) (Fig. 1). In contrast, durations of egg, larval, pupal and egg to adult periods of *S. albula* were similar on Bt and non-Bt soybean. However, survival of larvae, pupae and insects that completed their life cycle were reduced when fed Cry1Ac/Cry1F-soybean compared to non-Bt soybean.

When fed on Cry1Ac/Cry1F-soybean, significant reductions in larval weight of *S. eridania*, *S. cosmioides* and *S. albula* (from 52 to 71%, respectively) were observed (Table 2). Similar effects were observed for pupal weight of *S. eridania* and *S. cosmioides*, which weighed 16 and 25% less than pupae from larvae fed on non-Bt soybean. *Spodoptera albula* had similar pupal weights when larvae were fed Bt and non-Bt soybean (165.7 versus 167.5 mg, respectively). Females from *S. albula* and *S. cosmioides* produced similar numbers of eggs when their larval development occurred on Bt and non-Bt soybean. By contrast, *S. eridania* females oviposited 55% fewer eggs when larvae developed on Cry1Ac/Cry1F-soybean (Table 2).

## 3.2 Population growth parameters of *Spodoptera* species on Cry1Ac/Cry1F-soybean

A summary of the life table statistics for each *Spodoptera* species evaluated are shown in Table 3. The estimated population growth parameters indicated that *S. eridania* and *S. cosmioides* populations had higher development time (due to longer development time from neonate to adulthood on Bt soybean) and lower population increases (due to low larval survival and less eggs per female on Bt soybean) when fed on Cry1Ac/Cry1F-soybean (event DAS-44406-6 × DAS-81419-2) compared to non-Bt soybean. In contrast, *S. albula* presented similar development time and population increases on Bt and non-Bt soybean. Based on these results, females of *S. eridania* and *S. cosmioides* originating from larvae that fed on Cry1Ac/Cry1F-soybean produced less than 34 and 415 females per generation (*R₀*), respectively, in an average generation time (*T*) up to 58 days, while females of these species produced more than 178 and 607 females, respectively, in less than 49 days when fed on non-Bt soybean. *Spodoptera albula* produced a similar number of females on Cry1Ac/Cry1F-soybean as on non-Bt soybean over the same amount of time (156 versus 217 females per female, respectively). These results indicate that females from *S. eridania* and *S. cosmioides* produced 93 and 51% less females per generation, respectively, on Cry1Ac/Cry1F-soybean. When exposed to Cry1Ac/Cry1F-soybean, *S. eridania* and *S. cosmioides* populations also presented a rate of natural population increases lower than 0.07 and 0.10 (Table 3). These parameter values are indicative of population suppression of these species by Cry1Ac/Cry1F-soybean. In contrast, *S. albula* had similar intrinsic rates of population increase on Bt and non-Bt soybean.

### 4 DISCUSSION

The Cry1Ac/Cry1F-soybean variety tested in this study (containing events DAS-44406-6 × DAS-81419-2) reduced the survivorship, development and population growth of *S. eridania* and *S. cosmioides*. However, this Bt soybean had lower biological activity against *S. albula*. These results also indicated that all three *Spodoptera* species evaluated had lower susceptibility to Cry1Ac/Cry1F-soybean than other lepidopteran species, such as *A. gemmatalis*, *C. includens*, *C. virens*, and *H. armigera* which are the main target pests of this transgenic event. The relatively low biological activity of Cry1Ac/Cry1F Bt soybean on these Spodoptera species reflects their inherently low susceptibility to the Cry1Ac and Cry1F Bt proteins.

Similar results were observed for *S. eridania* fed on Cry1Ac/Cry1F-cotton. Previous studies also reported that *S. eridania* and *S. cosmioides* had naturally low susceptibility to Cry1Ac and Cry1F proteins in diet bioassays and to Cry1Ac-soybean and Cry1Ac-cotton. Consistent with these findings, other species from the *Spodoptera* genus including *S. frugiperda*, *S. exigua* (Hübner) and *S. littura* (F.) exhibited low susceptibility to Cry1Ac-soybean, Cry1Ac-cotton and Cry1Ac/Cry1F-cotton. The relative low susceptibility of *S. eridania*, *S. cosmioides* and *S. albula* to Cry1Ac and Cry1F may be influenced by the low affinity of these Bt proteins to midgut receptors, and faster protein degradation in the larval midgut. However, this may also be associated with the insufficient in planta expression of Bt proteins to control these species.

Our findings also indicate that distinct populations of *S. eridania* and *S. cosmioides* show similar but significant impacts on biological parameters when exposed to Cry1Ac/Cry1F-soybean. Similar effects on survivorship and development were also observed in populations of *S. frugiperda* fed on Cry1Ac-soybean, *C. includens* and *C. virens*, and Cry1Ac/Cry1F-cotton. In contrast, *S. eridania* and *S. cosmioides* had similar survivorship and development on Cry1Ac-soybean, Cry1Ac-cotton and non-Bt plants. The effects of Cry1Ac/Cry1F-soybean on immature stages of *S. eridania* and *S. cosmioides*, such as longer development time, lower survival and reduced eggs per female, affected population growth parameters,
causing population suppression of these species. In contrast, Cry1Ac/Cry1F-soybean did not significantly affect S. albula biological parameters compared to non-Bt plants. Within the IPM context, alternative strategies will be necessary to control Spodoptera species when significant infestation occurs on Cry1Ac/Cry1F-soybean under field conditions. The fact that S. albula biological parameters compared to non-Bt plants.

Figure 1 Duration and survival rates of Spodoptera species fed on leaves of Cry1Ac/Cry1F-soybean (event DAS-44466-6 × DAS-81419-2) and a non-Bt soybean isolate. Pairs of bars (± standard error) with different letters differ significantly by t-test (P < 0.05).

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Table 2 Biological parameters of *Spodoptera* species fed on leaves of Cry1Ac/Cry1F-soybean (event DAS-444Ø6-6 × DAS-81419-2) and a non-Bt soybean isolate

| Biological parameter | Cry1Ac/Cry1F-soybean | Non-Bt soybean | *P* Value |
|----------------------|-----------------------|----------------|-----------|
| *Spodoptera eridania* – Campo Verde, MT | Larval weight at 14 days (mg) | 111.7 ± 8.4 | 315.3 ± 30.2 | <0.0001 |
| Pupal weight (mg) | 195.5 ± 12.4 | 229.9 ± 2.9 | 0.0275 |
| Mean eggs/female | 845.3 ± 152.2 | 1440.8 ± 95.1 | 0.0099 |
| *Spodoptera eridania* – Quevedos, RS | Larval weight at 14 days (mg) | 145.0 ± 9.5 | 504.7 ± 36.5 | <0.0001 |
| Pupal weight (mg) | 176.8 ± 5.2 | 210.1 ± 2.2 | 0.0004 |
| Mean eggs/female | 522.60 ± 91.9 | 1159.0 ± 91.2 | 0.0007 |
| *Spodoptera cosmioides* – Santa Maria, RS | Larval weight at 14 days (mg) | 196.0 ± 6.8 | 403.1 ± 30.7 | <0.0001 |
| Pupal weight (mg) | 315.8 ± 6.8 | 347.9 ± 5.0 | 0.0023 |
| Mean eggs/female | 1852.7 ± 153.4 | 2284.1 ± 148.9 | 0.0547 |
| *Spodoptera cosmioides* – São Pedro, RS | Larval weight at 14 days (mg) | 138.8 ± 18.2 | 447.0 ± 31.7 | <0.0001 |
| Pupal weight (mg) | 309.2 ± 8.4 | 413.1 ± 10.2 | 0.0001 |
| Mean eggs/female | 2157.2 ± 102.7 | 2399.4 ± 148.9 | 0.0007 |
| *Spodoptera albula* – Sapezal, MT | Larval weight at 14 days (mg) | 159.7 ± 13.1 | 452.3 ± 9.7 | <0.0001 |
| Pupal weight (mg) | 165.7 ± 2.4 | 167.5 ± 2.0 | 0.5924 |
| Mean eggs/female | 990.3 ± 177.5 | 738.4 ± 87.4 | 0.1661 |

Note: Values represent means ± standard error. A separate *t*-test (*P* < 0.05) was conducted between Cry1Ac/Cry1F-soybean and the non-Bt soybean for each biological parameter.

Table 3 Comparison of population growth parameters of *Spodoptera* species fed on leaves of Cry1Ac/Cry1F-soybean (event DAS-444Ø6-6 × DAS-81419-2) and a non-Bt soybean isolate

| Spodoptera species | Population growth parameter | T (days) | *R*₀ (♀ / ♀) | *r*ₘ (♀ / ♀ × day) |
|-------------------|-----------------------------|----------|--------------|------------------|
| *Spodoptera eridania* – Campo Verde, MT | Cry1Ac/Cry1F-soybean | 52.38 ± 0.25 a | 12.64 ± 3.20 b | 0.05 ± 0.004 b |
| Non-Bt soybean | 43.85 ± 0.26 b | 178.94 ± 11.81 a | 0.14 ± 0.005 a |
| *Spodoptera eridania* – Quevedos, RS | Cry1Ac/Cry1F-soybean | 48.78 ± 0.24 a | 33.89 ± 5.94 b | 0.07 ± 0.004 b |
| Non-Bt soybean | 41.61 ± 0.99 b | 191.78 ± 35.01 a | 0.13 ± 0.002 a |
| *Spodoptera cosmioides* – Santa Maria, RS | Cry1Ac/Cry1F-soybean | 56.43 ± 0.22 a | 332.37 ± 27.52 b | 0.10 ± 0.002 b |
| Non-Bt soybean | 49.09 ± 0.22 b | 684.77 ± 45.66 a | 0.13 ± 0.001 a |
| *Spodoptera cosmioides* – São Pedro, RS | Cry1Ac/Cry1F-soybean | 58.09 ± 0.56 a | 415.47 ± 39.63 b | 0.10 ± 0.001 b |
| Non-Bt soybean | 42.60 ± 0.25 b | 607.05 ± 59.64 a | 0.15 ± 0.003 a |
| *Spodoptera albula* – Sapezal, MT | Cry1Ac/Cry1F-soybean | 47.18 ± 0.41 a | 156.64 ± 24.49 a | 0.11 ± 0.004 a |
| Non-Bt soybean | 46.73 ± 0.39 a | 217.81 ± 33.83 a | 0.12 ± 0.003 a |

Note: *T* is the mean length of a generation (in days); *R*₀ is the net reproductive rate (females per female per generation); *r*ₘ is the intrinsic rate of population increase (per day).

Means ± standard error within a column followed by the same letter in each *Spodoptera* species are not significantly different (*t*-tests for pairwise group comparisons, *P* > 0.05).

*eridania* and *S. cosmioides* fed Cry1Ac/Cry1F-soybean had reduced larval weight and increased developmental time to adulthood is favorable for management. Less healthy larvae with longer development times may make them more susceptible to natural enemies and entomopathogenic agents, which consequently would further reduce population growth, reducing the population density and outbreaks of *S. eridania* and *S. cosmioides* in Brazilian agricultural landscapes. Alternatively, the high adoption of Bt soybean with relatively low efficacy against secondary pests such as *Spodoptera* species may provide opportunities for these species.
to become more important in soybean. This can be favored by the competitive advantage of some Spodoptera species when competing with other noctuids, including Spodoptera frugiperda – which appears to show increased incidence in Bt soybean fields in recent seasons in Brazil.

Under field conditions, the Cry1Ac/Cry1F-soybean may provide population suppression of Spodoptera eridania and Spodoptera cosmioides, but little protection against outbreaks of Spodoptera albula. Thus, scouting for larvae and damage from these species on Cry1Ac/Cry1F-soybean will help decision making regarding the use of other IPM tactics. Chemical insecticides will likely be the main control tactic against Spodoptera species on this Bt soybean. Accordingly, if outbreaks of these species are verified it is recommended that insecticides be applied when local action thresholds are reached. In summary, to extend the benefits of Cry1Ac/Cry1F-soybean against lepidopteran pests that attack soybean, this biotech event must be combined with other IPM tools and robust IRM plans to prolong the durability of this soybean technology.

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