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TROPICAL SODA APPLE (*SOLANUM VIARUM*) MEDIATED COMPETITION VIA INDUCED RESISTANCE: INTERACTION BETWEEN *GRATIANA BOLIVIANA*, *SPODOPTERA EXIGUA* AND *FRANKLINIELLA OCCIDENTALIS*¹

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ABSTRACT

Survival assays were conducted with beet armyworm (BAW), *Spodoptera exigua* (Hübner), a tortoise beetle, *Gratiana boliviana* Spaeth, and western flower thrips (WFT), *Frankliniella occidentalis* (Pergande), on tropical soda apple (TSA), *Solanum viarum* Dunal, a relative of tomato. Both *S. exigua* and *G. boliviana* seem to induce plant defenses in tropical soda apple. Significantly more *S. exigua* neonate larvae survived to second instar on non-induced plants and artificial diet when compared with plants with induced defenses. Our results further suggest that the induced response in TSA was systemic, since BAW neonates suffered higher mortality in induced plants despite not being in direct contact with the damaged part of the plant. Results suggested that feeding action of *G. boliviana* on TSA had no significant influence on WFT host choice.

Key Words: induced resistance, secondary plant defenses, night shade, biological control

RESUMEN

Se realizó un ensayo de la supervivencia del gusano soldado de la remolacha (GSR), *Spodoptera exigua* (Hübner); un escarabajo tortuga, *Gratiana boliviana* Spaeth; y el trips occidental de las flores (TOF), *Frankliniella occidentalis* (Pergande) en *Solanum viarum* Dunal, una planta del mismo género del tomate conocida como chinchihua. Tanto *S. exigua* y *G. boliviana* parece inducir las defensas de las plantas de chinchihua. Un número significativamente mayor de las larvas recién nacidas de *S. exigua* sobrevivió hasta el segundo estadio en las plantas no inducidas y sobre la dieta artificial en comparación con plantas con defensa inducida. Nuestros resultados sugieren además que la respuesta inducida por la *S. viarum* fue sistémica, ya que las larvas recién nacidas de GSR sufren una mayor mortalidad en las plantas inducidas a pesar de no estar en contacto directo con la parte dañada de la planta. Los resultados sugieren que la acción de la alimentación de *G. boliviana* en *S. viarum* no tuvo influencia significativa en la elección del hospedero del trips (TOF).

Tropical soda apple, *Solanum viarum* Dunal (TSA) (Solanales: Solanaceae), is a serious invasive weed species, native to Argentina and Brazil. The plant was first reported in Florida in 1988 (Mullahey et al. 1993a), and has invaded both agricultural and natural ecosystems (Mullahey et al. 1993b; Mullahey & Akanda 1996). This weed spread rapidly and by 1996 it was estimated that 1 million acres of land in Florida were infested by TSA (Mullahey et al. 1996). TSA is an alternative host for key insect pests such as western flower thrips (WFT), *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), beet armyworm (BAW), *Spodoptera exigua* (Hübner), southern armyworm, *S. eridania* (Stoll) (Lepidoptera: Noctuidae) (Sudbrink et al. 1999; Hix et al. 2008), southern green stinkbug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae), Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Co-

leoptera: Chrysomelidae), tomato hornworm, *Manduca quinquemaculata* (Haworth) (Lepidoptera: Sphingidae), and silverleaf whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) (Habeck et al. 1996; Medal et al. 1999; Sudbrink et al. 1999). TSA also is known to host tomato spotted wilt virus and 6 other viruses that affect vegetable crops (McGovern et al. 1994; Hix et al. 2008).

In 2003, United States Department of Agriculture (USDA) approved the release of a biological control agent, *Gratiana boliviana* Spaeth (Coleoptera: Chrysomelidae), in Florida (Medal et al. 2003). This tortoise beetle is highly specific; it can only complete its life cycle on TSA plants (Medal et al. 2002). Both larval and adult stages of *G. boliviana* feed on TSA leaves, resulting in extensive defoliation (Medal et al. 2002). One of the ways solanaceous plants such as TSA respond to this

kind of insect herbivore feeding damage is by biosynthesis of proteinase inhibitors, which accumulate in vacuoles of uninjured plants cells and are deleterious to some caterpillars (Karban & Myers 1989).

Induced response may influence the fecundity of herbivore insects, their egg size and quality, and choice of oviposition sites (Awmack & Leather 2002). Unlike generalists, specialist herbivores are adapted to these novel plant defenses by detoxification or sequestering plant defense compounds; this adaptation may be why some induced defenses protect against generalist, but not specialist insect herbivores (Agrawal 1999). This herbivore induced plant resistance and its effect on competition between insects that share the same host plant has generated considerable interest on how this phenomenon may impact both agricultural and natural ecosystems (Karban & Baldwin 1997; Agrawal 1999; Lynch et al. 2006; Delphia et al. 2007; Hix et al. 2008).

Previous studies have shown that feeding on TSA by beet armyworm and southern armyworm induces secondary plant defenses that negatively affect the performance of other insect herbivores (Hix et al. 2008). Oral secretions from beet armyworm larvae contain N-(17-hydroxylinolenoyl)-L-glutamine (volicitin), an elicitor of plant secondary metabolites (Alborn et al. 1997). Specific objectives of this paper were to determine if prior feeding by *G. boliviana* has any negative effect on the performance of beet armyworm larvae. This study aims to enhance our understanding on how weed biological control agents may influence the performance of weeds as alternative hosts to other insects, especially thrips.

MATERIALS AND METHODS

Tropical soda apple plants were grown from seed collected from the field in Bainbridge, GA. They were sowed on seed bed trays and transplanted to 4-inch (10.2 cm) diam pots in an outdoor screen house at the USDA/ARS CMAVE and Florida A&M University (FAMU) Center for Biological Control research station, Tallahassee, Florida. Plants were watered regularly to make sure the plants had adequate moisture supply throughout. The *G. boliviana* colony was started from larvae obtained from the Florida Department of Agriculture and Consumer Services, Division of Plant Industry (FDACS, DPI), Fort Pierce, Florida. Beetles were maintained on TSA plants confined in an outdoor screen cage (2 × 2 × 2 m). A BAW colony was established from larvae and were maintained on artificial diet from Bio-Serv (Frenchtown, New Jersey).

This study was conducted in the growth chamber with a photoperiod of 14 L:10 D and temperature of 26°C. Secondary plant defense in TSA plants was induced by confining 3 third instar *G.*

boliviana to the third leaf of 40-d-old TSA plants in a modified aerated Petri dish. The side of the base of the Petri dish had a circular opening large enough to fit the stalk/petiole of a TSA leaf while the upper lid/cover had a 20-mm hole covered with thrips-proof screen for aeration. The Petri dish base was placed in such manner that the TSA leaf, still attached to the plant, could be contained with the petiole passing through the circular opening. Three third instar beetle larvae were added to the leaf and the Petri dish was then covered with the aerated lid and sealed with parafilm and modeling clay to prevent escape. This Petri dish unit was then secured in place by gluing a thin bamboo dowel to its base and inserting the unit into the soil. Beetle larvae were allowed to feed on TSA for 3 d during which time they consumed 50 to 100% of the leaflet. TSA plants assigned to the control treatment had no beetle feeding. Larvae used to damage TSA were removed from the plants before assaying for induced resistance; insects used to induce resistance were not allowed to interact with BAW used to assay for resistance.

Beet Armyworm Neonate Survival

To assess the effect of induction on BAW neonate mortality, 10 BAW neonates were placed and confined after the 3-d beetle feeding period on the leaf opposite the third leaf of each induced and non-induced plants by using a small paintbrush. The BAW neonates were confined to TSA leaves by the same method used to confine the third instar *G. boliviana*, as described above. Ten induced TSA plants and 10 control plants were replicated in the experiment. On the fifth d of BAW feeding, the number of BAW larvae alive on non-induced and on induced TSA were counted and recorded. Data was analyzed using Student's *t*-test. All statistical analyses were performed with SigmaPlot 11.2 (Systat Software, Inc., San Jose, California).

Western Flower Thrips Host Choice Assay

Tropical soda apple plants were wounded by confining 3 third instar *G. boliviana* on the third leaf of each of 8 flowering TSA plants. After 3 d, a pair of flowers from damaged plants and a pair from undamaged plants (control) were excised with a razor blade and placed in each of 8 sealed Petri dishes, as described by Stout & Duffey (1996). Ten adult WFT were placed in the center of each Petri dish. The sealed petri dishes were placed in a growth chamber with a photoperiod of 16 L:8 D at 27°C. After 24 h the flowers were collected, and with the aid of a dissecting microscope, the number of WFT on induced and non induced flowers were counted and recorded. Data were analyzed by Student's *t*-test.

Western Flower Thrips Oviposition

After the 3-d feeding period by third instar *G. boliviana* on the third leaf of TSA, 10 female adult WFTs were introduced and confined on the leaf opposite the third leaf of 5 *G. boliviana*-induced and 10 placed on 5 control (non-induced) plants under a photoperiod of 16 L: 8 D at 27°C. After 48 h, TSA leaves were collected and stained for thrips eggs with the staining technique described by Backus et al. (1988). Data were analyzed by Student's *t*-test.

RESULTS AND DISCUSSION

Feeding by insect herbivores, including BAW, on solanaceous plants has been noted to induce plant secondary plant defenses (Stout & Duffey 1996; Agrawal 1999; Hix et al. 2008). We hypothesized that feeding on TSA by *G. boliviana*, a specialist biological control agent, will elicit the production of plant defense compounds that will negatively influence BAW neonate survivorship and thrips oviposition and host choice. Feeding action of *G. boliviana* third instars on the third leaf of TSA had a substantial effect on the survival of BAW neonates. After 5 d, survivorship of BAW neonates placed on non-induced TSA plants (2.1 ± 0.28 SE) was greater than that of neonates placed on *G. boliviana*-induced TSA plants (0.4 ± 0.16 SE) ($t = 5.50$, $df = 18$, $P < 0.0001$) (Fig. 1A).

These results are in general agreement with a study that evaluated BAW neonate survival on TSA induced by third instar BAW (Hix et al. 2008), and in another study done with tomatoes, where BAW suffered increased mortality when fed on plants induced by corn earworm *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) feeding (Stout & Duffey 1996). The difference in survival rate between the BAW neonates placed on induced plants and those placed on control plants could be attributed to changes in plant chemistry. TSA plants have been shown to elevate polyphenol oxidase (PPO) enzyme levels when fed on by *S. exigua* and *S. eridania* (Hix et al. 2008). PPO is an enzyme that oxidizes phenolics to quinones, and it is known to play a defensive role against insects (Bhonwong et al. 2009). Our results further suggest that the induced response in TSA was systemic, because BAW neonates suffered higher mortality in induced plants despite not being in direct contact with the damaged part of the plant.

Our results further showed that feeding action of *G. boliviana* on TSA had no significant influence on WFT host choice when given a choice between flowers from induced TSA (0.43 ± 0.13 SE), and non-induced TSA (1.3 ± 0.43 SE), ($t = 1.36$; $df = 12$; $P = 0.083$) (Fig. 1B). Prior to this research, it

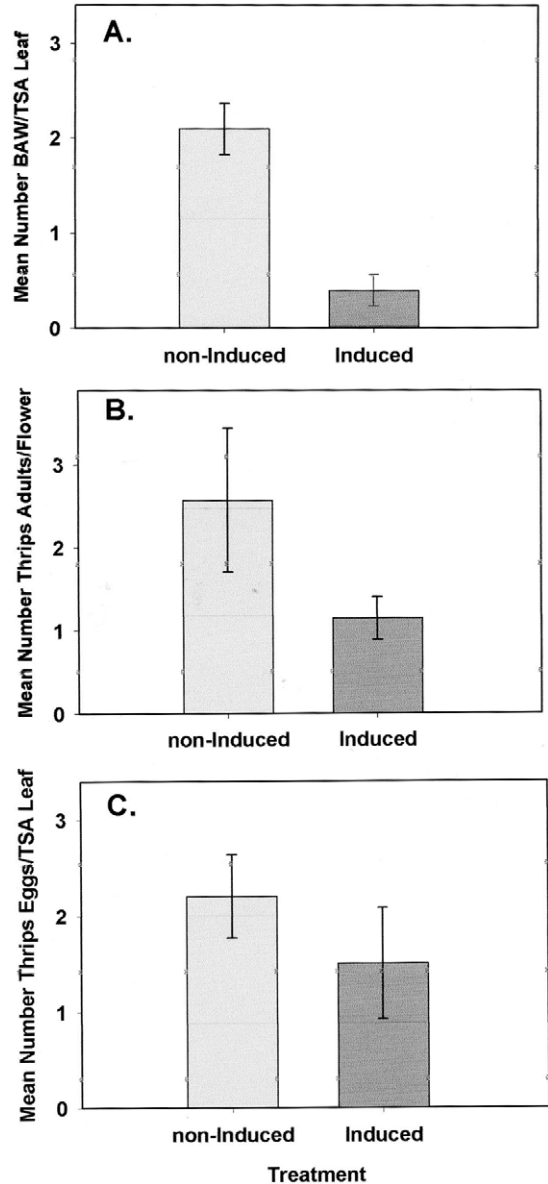


Fig. 1. Effects of feeding on *Solanum viarum* (TSA) by *Gratiana boliviana* on *Spodoptera exigua* (BAW) and *Frankliniella occidentalis*. A. Survivorship in numbers (\pm SE) of BAW placed on control plants (non-induced) and *G. boliviana* induced plants as neonates for 5 d. Significantly more BAW larvae survived on non-induced plants than *G. boliviana* induced plants ($P = 0.0001$). B. Western flower thrips (WFT) *F. occidentalis* host choice in number of adult thrips per TSA flower (\pm SE) using induced TSA flowers and non-induced TSA flowers (control) in a free choice situation ($P = 0.083$). C. Western flower thrips (WFT) *F. occidentalis* oviposition performance in number of eggs (\pm SE) per TSA leaf. There was no statistical difference in oviposition after 48 h ($df = 8$; $P = 0.81$).

was not known whether WFT can actually lay eggs on TSA leaves. While studying the impact of *G. boliviana* on WFT oviposition via induced resistance, we were able to confirm that WFT does oviposit on TSA foliage. We found that oviposition by the thrips on induced TSA leaves (2.2 ± 0.43 SE) was not significantly different from oviposition on non-induced plants (1.5 ± 0.58 SE) ($t = 0.24$; $df = 8$; $P = 0.81$) (Fig. 1C). We observed that trichomes on the surface of TSA leaves produced sticky glandular exudates which greatly restricted mobility and caused mortality of both adult and larval stages of WFT. This defensive trait may pose a great challenge on induced resistance behavioral bioassays involving small insects like WFT. WFT required 48 h at 27°C for oviposition on TSA, and immature WFT failed to become adults on control plants or induced plants.

Uninfected adult WFT cannot vector plant viruses even when they feed on infected hosts due to the presence of a midgut barrier (Ullman et al. 2004). Recent studies by Moritz et al. (2004) showed that acquisition of tospovirus by thrips is restricted to first and early second instars because this is the only time period in WFT development cycle when there is a temporary association between midgut, visceral muscles, and salivary glands. This association is the result of a displacement of the brain into the prothoracic region by enlarged cibarial muscles (Moritz et al. 2004). In the late second instar the brain is repositioned in the head, and so the intimate contact between the midgut, visceral muscles, and salivary glands is lost (Moritz et al. 2004). Thus, only plants that are susceptible to TSWV and suitable reproductive hosts of WFT can serve as sources for spread of TSWV (Ullman et al. 1997). WFT is known to feed on over 250 crop plants and numerous uncultivated plants, which make it important to distinguish the plants it can reproduce on because it feeds on many species on which it cannot reproduce (Reitz 2009). These data suggest that it would be difficult for TSA leaves to produce infective WFT adults unless flowers are present. The absence of TSA flowers from June through August in Florida may help limit the spread of this and other viruses from TSA to other plants.

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