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DOES SECONDARY PLANT METABOLISM PROVIDE A MECHANISM FOR PLANT DEFENSES IN THE TROPICAL SODA APPLE *SOLANUM VIARUM* (SOLANALES: SOLANACEAE) AGAINST *SPODOPTERA EXIGUA* AND *S. ERIDANIA* (LEPIDOPTERA: NOCTUIDAE)?

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Abstract

Survival assays were conducted with beet armyworm *Spodoptera exigua* (Hübner) and southern armyworm *S. eridania* (Stoll) with tropical soda apple *Solanum viarum* Dunal, a relative of tomato. In addition, polyphenol oxidase (PPO) enzyme assays were conducted to determine if plant defense compounds are being produced by tropical soda apple in response to herbivory. Both *S. exigua* and S. *eridania* induced plant defenses in tropical soda apple. Significantly more *S. exigua* and *S. eridania* neonate larvae survived to 2nd instar on non-induced plants and artificial diet when compared with plants with induced defenses. Tropical soda apple plants fed on by *S. exigua* and *S. eridania* had significantly increased PPO activity.

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

Resumen

Se condujeron analisis de supervivencia con palometas de *Spodoptera exigua y* palometas surenas de *S. eridana* en manzana de soda tropical *Solanun viarum* relativa del tomate. Mas aun, analisis con enzimas de oxidasa de polyphenol (PPO) fueron realizaron para determinar si se produce compuestos secundarios como defensa de la planta de manzana de soda tropical en respuesta a herviboros. Tanto *Spodoptera exigua* como *S. eridana* parecen inducir en la planta defensas secundarias. Significativamente mas larvas neonatas de *S. exigua* y *S. eridana* sobrevivieron al segundo estadio en plantas no inducidas y dietas artificiales comparadas con plantas con defensas inducidas. Las plantas de manzana de soda tropical alimentadas *con S. exigua y S. eridana* han aumentado significartivamente la actividad de PPO.

Translation provided by the authors.

The tropical soda apple (TSA) *Solanum viarum* Dunal is a nightshade classified by the State of Florida (FLEPPC 2007) and the USDA as a noxious weed. Tropical soda apple is native to Argentina, Brazil, Paraguay, and Uruguay (Gandolfo et al. 2007) and was first reported in Florida in 1988 (Mullahey et al. 1993). It has invaded thousands of acres of pasture thereby reducing carrying capacity, and has invaded natural areas displacing native plant species (Mullahey & Colvin 1993; Medal & Cuda 1999). Tropical soda apple serves as a reservoir for several viruses including the tomato spotted wilt virus (TSWV) vectored by thrips including *Frankliniella occidentalis* (Pergande), the western flower thrips.

Insect herbivory can have effects on both the plant and the herbivore. For example, tomato plants respond to herbivory by producing proteinase inhibitors that reduce the palatability and nutritional quality of the plant. These plant defense compounds are directed by the octadecanoid pathway (Karban & Baldwin 1997; Thaler 1999a, 1999b). Herbivore feeding has been found to induce peroxidase, lipoxygenase, polyphenol oxidase (PPO) and proteinase inhibitor (PI) activities (Stout et al. 1998) but not necessarily all at the same time by a given insect. This induced resistance (IR) system directed by the octadecanoid pathway is triggered by jasmonates such as jasmonic acid by the feeding of a broad range of insects (Broadway & Duffey 1986; Karban & Baldwin 1997). These induced defense proteins can reduce insect fitness, host preference, and nutritional value as well as increase mortality and work independently of constitutive defenses. Plants produce more than 1000 different volatiles by various plant species which may attract parasitoids and predators that attack the herbivore. These include the "green-leaf" 6-carbon aldehydes, alcohols and derivatives as well as alkanes, alkenes, alcohols, ketones, aldehydes, ethers, esters, and carboxylic acids just to name a few. Many of them are not species specific while others are very specific in

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which species they attract (D'Allessandro & Turlings 2005).

The beet armyworm *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) was chosen because it is a generalist herbivore known to induce secondary plant defenses in tomato, a closely related species in the genus *Solanum* (Felton et al. 1992; Alborn et al. 1997; Alborn et al. 2000). The southern armyworm *Spodoptera eridania* (Stoll) was chosen for this study due to its range overlap with TSA in Florida (R.L.H. unpublished data). The objectives of this study were to determine if feeding by the generalist herbivores *S. exigua* and *S. eridania* (Stoll) induced secondary plant defenses in TSA.

Materials and Methods

Spodoptera exigua colonies were established from eggs obtained from Bio-Serv (Frenchtown, NJ) and *S. eridania* colonies were established from wild caterpillars collected feeding on tomato. Colonies were maintained on *S. exigua* artificial diet (Bio-Serv, Frenchtown, NJ). Prior to assays, caterpillars were allowed to feed on tomato for 24 h.

Tropical soda apple plants were grown from seed collected from wild plants in Leon Co., Florida. Plants were planted in pots (12.7 cm × 12.5 cm) with Metro Growing Mix 220 (Sierra Grace Hort Products, Milpita, CA) (Mullahey & Cornell 1994) and fertilized with Peters® 20-20-20 (N) solution and maintained in an environmental chamber with photoperiod of 16:8 (L:D) or an outdoor shade tent.

Five 4th instars of *S. exigua* were allowed to feed on 5 TSA plants (i.e., 5 larvae per plant) for a period of 3 d. These plants were 45 d old. After this "induction" period, 100 neonate *S. exigua* larvae were placed on each of 5 induced plants, 5 control plants, and an external control consisting of *S. exigua* artificial diet (BioServ, Frenchtown, NJ). Those molting to the second instar were quantified. Plants were in individual cages to prevent caterpillars from moving from plant to plant.

This experiment was conducted in the same way substituting *S. eridania* in place of *S. exigua*. This experiment was repeated twice for *S. exigua* and *S. eridania*. Means and standard errors were calculated and subjected to ANOVA followed by Tukey's HSD where appropriate ($\alpha = 0.05$). Statistical analyses were done with JMP IN (SAS Institute 1996).

Polyphenol Oxidase Assay

Five 4th instars of *S. exigua* were placed on each of eight 45-d-old TSA plants, and five 4th instars of *S. eridania* larvae were placed on each of eight 45-d-old plants. The control consisted of eight 45-d-old plants that had never been exposed to herbivores. After 2 d of feeding, a leaf from each plant was excised at the petiole with a razor blade (n = 8). PPO activity was quantified by the methods of Felton et al. (1989). The rate of reaction was determined with a spectrophotometer (BioTek) to measure absorbance at 470 nm every 10 s over 3 min. This reaction rate was then divided by the mass of the leaf cutting to determine the rate for that cutting (n = 8). The arcsine-square root transformation was used on the mean rates and subjected to ANOVA followed by Tukey's HSD (α = 0.05).

Results

Significantly more neonate *S. exigua* larvae survived to 2nd instar on the non-induced tropical soda apple and artificial diet than on induced TSA ($F = 12.8, df = 2, 14; P = 0.001$). The mean number surviving on the artificial diet was 91.0 (± 7.3 SEM), on non-induced plants 74.6 (± 12.3 SEM), and on induced plants 27.3 (± 9.75 SEM) (Fig. 1A). This experiment was repeated with similar results ($F = 12.6, df = 2, 14; P = 0.001$) (Fig. 1B). The mean survival on the artificial diet was 95.4 (± 6.2 SEM), on non-induced plants 69.1 (± 11.9 SEM), and on induced plants 30.2 (± 8.8 SEM).

Significantly more neonate *S. eridania* larvae survived to the 2nd instar on the non-induced TSA and artificial diet than did on induced plants ($F = 11.0, df = 2, 14; P = 0.002$). The mean survival on the non-induced plants was 67.16 (± 8.1 SEM), on artificial diet 93.3 (± 5.9 SEM), and on induced plants 34.0 (± 10.3 SEM) (Fig.2A). This experiment was repeated with similar results ($F = 7.4$, $df = 2, 14; P = 0.008$) (Fig. 2B). The mean survival on the artificial diet was 89.0 (± 8.1 SEM), on non-induced plants 80.0 (±10.9 SEM) and on induced plants 29.0 (± 15.5 SEM).

Polyphenol Oxidase Assay

The PPO activity for both *S. exigua* and *S. eridania* induced plants was statistically different than the non-induced plants ($P < 0.008$ and $P < 0.003$, respectively), but means were not different from each other ($P < 0.868$). ANOVA was performed on transformed data ($F = 8.9, df = 2, 23; P = 0.002$). The data in Fig. 3 are the untransformed data.

Discussion

Before this study, nothing was known about secondary plant defenses in tropical soda apple. We hypothesized that feeding by generalist and/or specialist herbivores will induce secondary plant defenses in TSA. Survival assays were conducted with beet armyworm and southern armyworm because these generalist herbivores are known to induce secondary plant defenses in to-

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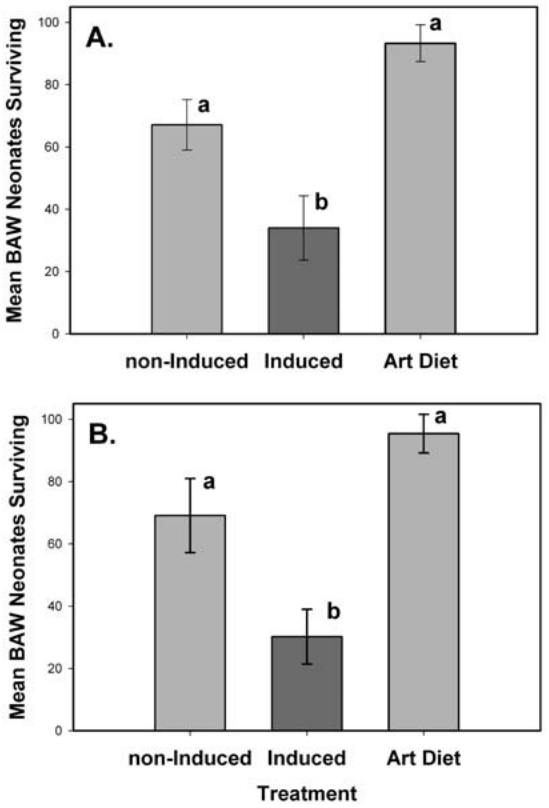


Fig. 1. A. Mean number (± SEM) of neonate *Spodoptera exigua* surviving to 2nd instar on non-induced TSA were significantly higher than on induced TSA plants ($P < 0.038$). Tukey's HSD $n = 5$, $\alpha = 0.05$. B. The mean number of neonate larvae surviving to 2nd instar was significantly higher on non-induced plants than induced plants ($P < 0.029$). Tukey's HSD $n = 5$, $\alpha = 0.05$. The artificial diet means and non-induced plant means were not statistically different in either experiment ($P > 0.106$ and $P > 0.153$ for A and B, respectively). Means followed by the same letter are not significantly different.

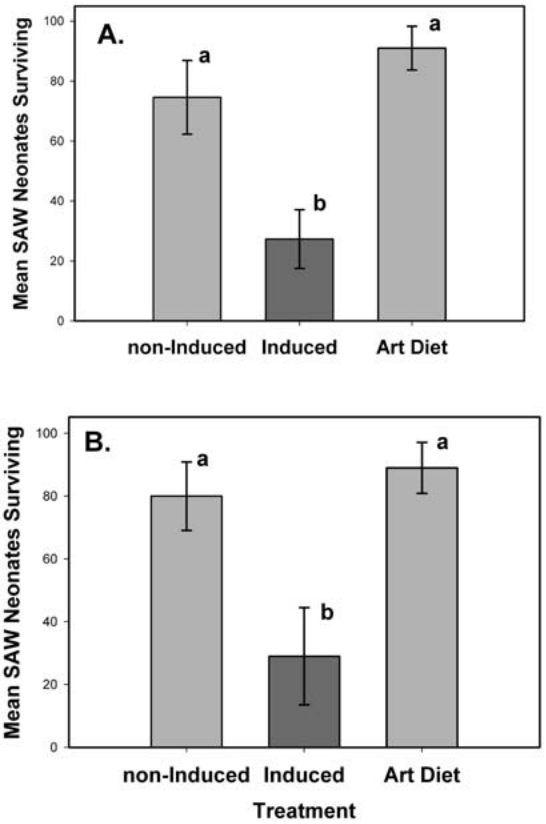


Fig. 2. A. Mean number (± SEM) of neonate *Spodoptera eridania* surviving to 2nd instar on non induced TSA were significantly higher than on induced TSA plants ($P < 0.015$). Tukey's HSD $n = 5$, $\alpha = 0.05$. B. Mean number of neonate larvae surviving to 2nd instar was significantly higher on non-induced plants than induced plants ($P < 0.026$). Tukey's HSD $n = 5$, $\alpha = 0.05$. The artificial diet means and non-induced plant means were not statistically different in either experiment ($P > 0.498$ and $P > 0.856$ for A and B, respectively). Means followed by the same letter are not significantly different.

mato, a relative of TSA. In addition, polyphenol oxidase (PPO) enzyme assays were conducted to determine if secondary plant defense compounds are being produced in response to herbivory. This oxidative enzyme is produced by solanaceous plants including tobacco and tomato (Stout et al. 1996; Thaler et al. 1996; Stout et al. 1998; Thaler 1999a). PPO reacts with substrates in the herbivore gut making essential amino acids unavailable (Duffey & Felton 1989; Felton et al. 1992; Halitschke et al. 2001). Based on our results, TSA plants fed on by *S. exigua* and *S. eridania* had significantly increased PPO activity. Both *S. exigua* and *S. eridania* appears to induce secondary plant defenses in TSA.

The tortoise beetle *Gratiana boliviana* Spaeth (Coleoptera: Chrysomellidae) was released in Florida in 2003 as a classical biological control agent of TSA (Medal et al. 2003). *G. boliviana* and other biological control agents in quarantine are specialists that only feed on this species. These species-specific agents may provide negative effects on *F. occidentalis* feeding, egg laying performance or vector competency. Tropical soda apple is known to be a host of tomato spotted wilt virus (TSWV). Generalist herbivores like *F. occidentalis* may demonstrate lower feeding preference for plants with induced plant defenses (Karban & Baldwin 1997; Gouinguene et al. 2003). We are currently

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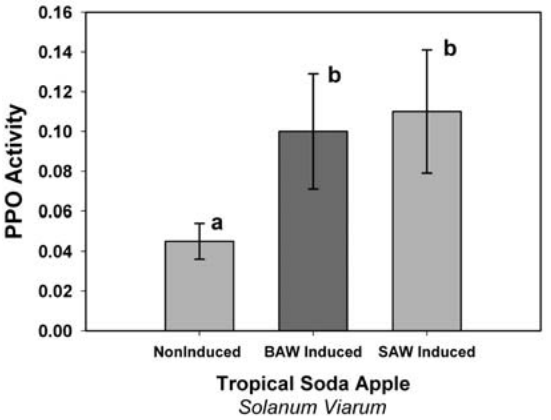


Fig. 3. The mean PPO level of *Spodoptera exigua* induced and *S. eridania* induced tropical soda apple leaves were significantly higher than the non-induced plants ($P < 0.008$ and $P < 0.003$, respectively). Tukey's HSD $n = 8$, $\alpha = 0.05$.

studying tropical soda apple induced responses in context of *G. boliviana*, *S. exigua*, and *F. occidentalis*.

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