Influence of Sun and Shade Conditions on Gratiana boliviana (Coleoptera: Chrysomelidae) Abundance and Feeding Activity on Tropical Soda Apple (Solanaceae) Under Field Conditions

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Influence of sun and shade conditions on *Gratiana boliviana* (Coleoptera: Chrysomelidae) abundance and feeding activity on tropical soda apple (Solanaceae) under field conditions

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Tropical soda apple, *Solanum viarum* Dunal (Solanaceae), is an invasive perennial broadleaf weed that is listed on the federal list of noxious weeds (USDA-APHIS 2010) and has become a serious problem in both agricultural and natural areas of the southeastern USA (Mullahey et al. 1993b; Mullahey 1996). This species is native to Paraguay, Uruguay, Argentina, and southern Brazil (Mullahey et al. 1993a). The earliest record of this plant in the USA was reported in 1988 in Glades County, Florida (Mullahey et al. 1993a). Dense stands of this prickly shrub engulf both open areas of pasturelands and shaded areas under tree canopies (Mullahey et al. 1998). The dense stands reduce stocking rates and restrict access of cattle to shade, resulting in production losses due to heat stress (Mullahey et al. 1998; Overholt et al. 2009). In 2003, the United States Department of Agriculture approved the release of a biological control agent, *Gratiana boliviana* Spaeth (Coleoptera: Chrysomelidae), against tropical soda apple (Gandolfo et al. 2007).

Some insects are more abundant and feed more on unshaded plants (Batch 1984; Lincoln & Mooney 1984), whereas other insects are more damaging to shaded plants (Bryant et al. 1983). Several hypotheses have been offered in the literature to explain the above variations. The carbon–nutrient balance hypothesis predicts that when carbon availability is limited relative to nitrogen, such as in shaded plants, concentrations of carbon-based defense metabolites decrease relative to nitrogen, thus increasing leaf palatability (Bryant et al. 1983). Conversely, in unshaded plants, where carbon-based defense chemicals are expected to be in relatively higher concentrations than in shaded plants, leaf palatability to herbivores decreases. An alternative hypothesis suggests that variation in abundance of host-specific herbivores on plants in open and shaded areas may be due to physiological constraints or behavioral responses of herbivores, or to the presence of natural enemies (Collinge & Louda 1988). Our study was conducted to determine whether the abundance and feeding activities of *G. boliviana* were influenced by exposure of plants to sun or shade conditions.

A survey was conducted during the fall of 2009 on a cattle ranch located in Madison County, Florida (30.4029167°N, 83.4570000°W). Tropical soda apple had been present on the ranch for approximately 8 yr, and *G. boliviana* adults were first released at the site in Jun 2009; 3,850 beetles were released from Jun to Sep (S. Hight, unpublished data). Plants were sampled every 5 m along 50 m transects. Sampling was conducted on 3 dates at 2 wk intervals. Four transects for the 1st sampling date were placed along the cardinal directions, originating from the center of a heavy tropical soda apple infestation, occurring in both shaded and unshaded areas, and supporting an established population of *G. boliviana.* On the 2nd and 3rd sampling dates, the 4 transects were placed at 22° and 44°, respectively, in a clockwise direction from the initial transects. The following parameters were measured or estimated for each selected plant: exposure to sun (unshaded, partially shaded, or completely shaded); leaf damage due to *G. boliviana*, scored on a scale of 0 to 5 as described by Overholt et al. (2009); and number of beetles. Plants were categorized as unshaded if they grew in open areas and were exposed to direct sunlight throughout the day; partially shaded if they grew at the margins of areas covered by tree canopies and were not exposed to direct sunlight for the whole day; and shaded if they grew under tree canopies and were not exposed to direct sunlight at any time of the day.

Abundance of adults and larvae of *G. boliviana* differed significantly among shaded, partially shaded, and unshaded tropical soda apple plants (Table 1) (adults: F = 20.82; df = 2,26; P < 0.0001; larvae: F =

Table 1. Mean (± SE) *Gratiana boliviana* abundance per tropical soda apple plant at 3 light conditions: unshaded, partially shaded, and fully shaded, at a ranch in Madison County, Florida.

Stage	Sun exposure	Mean ± SE[a]
Adult	Unshaded	3.2 ± 0.74A
	Partially shaded	1.4 ± 0.49AB
	Shaded	0.3 ± 0.22B
Larva	Unshaded	4.1 ± 1.18a
	Partially shaded	1.6 ± 0.56a
	Shaded	0.2 ± 0.12b

[a]Means ± SE for all 3 sampling dates. Means for each insect life stage followed by the same letter are not significantly different (P > 0.05; ANOVA, Tukey's HSD).

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13.05; df = 2,26; $P = 0.0001$). Adult and larval abundance were significantly higher on unshaded plants than on shaded plants (Tukey's HSD, $P < 0.05$). Feeding damage on the leaves was significantly higher on plants growing under full sun (unshaded) than on those plants growing under shaded conditions beneath tree canopies ($H = 17.970$; df = 2; $P = 0.001$: Kruskal–Wallis, Dunn's test) (Fig. 1).

Our results agree, in part, with the findings of Diaz et al. (2011), who also evaluated *G. boliviana* responses to tropical soda apple in unshaded and shaded conditions. In a greenhouse trial where beetles had no choice between plant type, Diaz et al. (2011) found greater feeding and higher beetle fitness on shaded plants, different from our result. However, field samples by Diaz et al. (2011) identified greater insect abundance on unshaded plants (similar to our result), but unshaded plants had less feeding damage than plants in the shade whereas our unshaded plants had more feeding damage than shaded plants.

Our results contrast with predictions of the carbon–nutrient hypothesis that shading increases leaf palatability to herbivores (Bryant et al. 1983), but they are consistent with several other studies that show specialist insects like *G. boliviana,* have greater abundance and feeding damage on unshaded plants than on those in the shade (Louda & Rodman 1996, Mooney et al. 2009). The greater feeding damage to unshaded plants could be due to higher *G. boliviana* abundance on unshaded tropical soda apple plants (Table 1) and/or the adaptation of *G. boliviana* to tropical soda apple plant defenses. For instance, defensive trichomes on tropical soda apple are larger and denser on unshaded plants (Diaz et al. 2011), similar to other solanaceous plants (Kennedy et al. 1981; Franca & Tingey 1994). These defensive trichomes are detrimental to most phytophagous insects; however, to *G. boliviana* larvae, trichomes are essential structures that must be present for a plant to be a suitable host (Gandolfo 2000). The *G. boliviana* larvae require the trichomes to grip and move successfully on the leaf surface of tropical soda apple plants (Gandolfo 2000). In general, plant defenses are not detrimental to most specialized insect herbivores because most have evolved methods to overcome these defenses (Agrawal 1999; Stotz et al. 2000).

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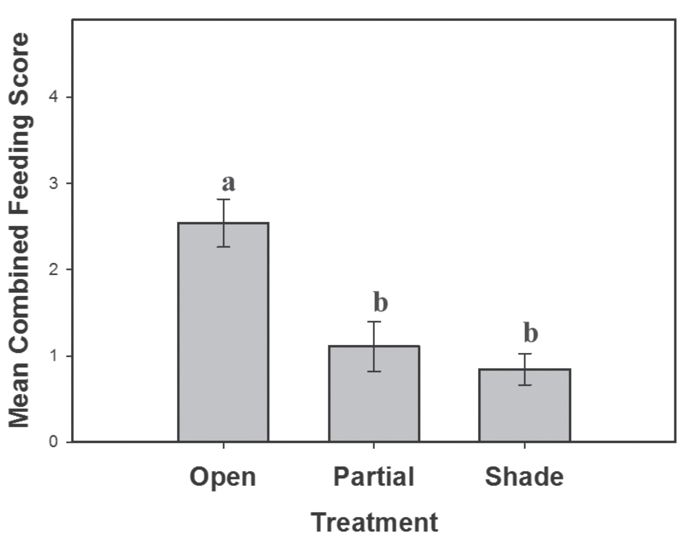

Fig. 1. Mean feeding damage score (± SE) for all 3 sampling dates caused by *Gratiana boliviana* beetles to tropical soda apple plants under 3 light conditions: unshaded, partially shaded, and shaded. Means with the same letter are not significantly different ($P < 0.05$: Kruskal–Wallis, Dunn's test).

Summary

Tropical soda apple is a perennial invasive weed species that has become a serious problem in both agricultural and natural areas of the southeastern United States. A field survey was conducted at a ranch in Madison County, Florida, to assess the effect of sun and shade conditions on the abundance and feeding activity of *Gratiana boliviana* Spaeth (Coleoptera: Chrysomelidae) on tropical soda apple. The results revealed that beetle abundance and their feeding damage were greater on plants growing in full sun exposure than on plants growing in shaded habitat.

Key Words: invasive species; biological control; insect herbivory; *Solanum viarum*

Sumario

La manzana de soda tropical es una especie de maleza invasora perenne que se ha convertido en un problema grave en las zonas agrícolas y naturales del sureste de los Estados Unidos. Se realizó un estudio de campo en un rancho en el condado de Madison, Florida, para evaluar el efecto de las condiciones de sol y sombra sobre la abundancia y actividad de alimentación de *Gratiana boliviana* Spaeth (Coleoptera: Chrysomelidae) en la manzana de soda tropical. Los resultados revelaron que la abundancia y su daño de alimentación por los escarabajos fueron mayores en las plantas que crecen expuestas a pleno sol que en las plantas que crecen en un hábitat sombreado.

Palabras Clave: especie de maleza invasora; control biológico; insecto herbivoro; *Solanum viarum*

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