Toxicity and Repellency of *Tephrosia candida* to Larval and Adult Diaprepes Root Weevil (Coleoptera: Curculionidae)

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J. Econ. Entomol. 96(3): 811–816 (2003)

ABSTRACT Leaves of the tropical legume *Tephrosia candida* DC deterred feeding by adults of the Diaprepes root weevil, *Diaprepes abbreviatus* (L.), compared with leaves of *Citrus macrophylla* Wester, a common citrus rootstock, or *T. vogelii* Hook. f. When larvae were placed in pots containing plants of the three species for 28 d in a growth chamber, larval survival and weight gain were significantly reduced in pots containing plants of *T. candida* compared with larvae in pots with *C. macrophylla* or *T. vogelii.* Diet incorporation of lyophilized roots of *T. candida* into an artificial diet increasingly inhibited the growth of larvae and increased larval mortality with increased concentration of roots, whereas roots from *C. macrophylla* or *T. vogelii* had no effect compared with the diet-only control. *T. candida,* but not *T. vogelii*, contains at least one constituent that acts as an antifeedant toward adult *D. abbreviatus* and as a toxicant toward larvae. No antifeedant effect of roots of *T. candida* toward larvae was observed in no-choice pot tests or in a diet incorporation bioassay. In pots, larval feeding damage to roots of *T. candida* was evident. In the diet incorporation assay, 97% of larvae survived 29 d on a diet of cellulose powder (a nutritionally inert filler) despite losing weight. We conclude that decreased survival and weight gain of larvae-fed fresh or lyophilized roots of *T. candida* were the result of ingestion of a toxicant and not deterrence from feeding.

KEY WORDS Citrus, *Diaprepes abbreviatus*, cover crops, antibiosis, antifeedant

THE DIAPREPES ROOT WEEVIL, *Diaprepes abbreviatus* (L.), has become a major threat to the sustained profitability of citrus production in the state of Florida and the Caribbean region. Because of its high degree of polyphagy and lack of effective natural enemies, this weevil is becoming increasingly abundant in Florida, has recently become established in Texas (Texas Department of Agriculture 2001), and threatens California through movement in container-grown ornamentals and other methods of shipment. Adult weevils can cause significant defoliation when present in large numbers, as commonly occurs in Puerto Rico, southern Florida, and, occasionally, in the Treasure Coast region of southeastern Florida (S.L.L., unpublished data). Larval feeding on the root cortex is considered of greater significance and can result in tree death by girdling the principal root or by providing infection courts for root-rot pathogens (*Phytophthora* spp.) (Rogers et al. 1996).

Currently available control options for Diaprepes root weevil in citrus are limited to foliar spraying for adults, entomopathogenic nematodes for larvae, and soil insecticides. Entomopathogenic nematodes require special care in application, and vary in efficacy as a result of edaphic and other factors (McCoy et al. 2002, Shapiro et al. 2000). The danger of groundwater contamination limits use of soil insecticides. Classical biological control is being attempted through introduction of egg parasitoids from the Caribbean (Hall et al. 2001). Additional options are needed as components of an integrated control strategy.

Leguminous cover crops can contribute to increased and sustainable crop productivity through erosion and weed control, biological nitrogen fixation, and by providing refuge for natural enemies of arthropod pests (Hokkanen 1991). Cover crops, such as perennial peanut (*Arachis* spp.), have been suggested for use in citrus groves (Prine et al. 1981). The growth of larval *D. abbreviatus* was measured on roots of three legume species and found to be equivalent to the growth of larvae reared on citrus in the case of *Arachis pintoi* Krapovickas & Gregory (perennial peanut) and *Crotalaria pallida* Ait. (rattlebox), or considerably greater than that on citrus in the case of pigeon pea, *Cajanus cajan* Millspaugh (Lapointe 2003). Of greater value would be a leguminous cover, mulch, or green manure that is also repellent or toxic to adults or larvae.

Fennah (1938, 1942) observed that the tropical legume *Tephrosia candida* DC contains a toxic principle in its seeds, stems, roots, and leaves. He also observed

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the plant was unattractive to adult Diaprepes root weevils. Species of *Tephrosia* are known to be sources of a number of compounds with toxic and deterrent activity toward insects (Machocho et al. 1995, Morris 1999, Simmonds et al. 1990). One of the best known species of this genus, *T. vogelii* Hook. f., is a source of rotenoids, including rotenone, tephrosin, and deguelin. This species at one time was the focus of a USDA–ARS program to increase leaf rotenoid content through breeding for production of insecticide and piscicide (Barnes et al. 1967, Gaskins et al. 1972).

Tephrosia candida has been used in mixed cropping regimes and as a fallow crop in tropical production systems in Vietnam (Fagerström et al. 2001) and India (Basu and Gupta 1988) where it is valued for its contribution to soil fertility. *T. candida* has been shown to contain phytochemicals that may have insecticidal or antifeedant properties (Kole et al. 1992; Andrei et al. 1997, 2002). This report describes the response of adult Diaprepes root weevil to foliage of *T. candida* and *T. vogelii,* and the survival and weight gain of larvae, when allowed to feed on the roots of potted plants and on artificial diet containing root powder of these species.

Materials and Methods

Plants. Seed of *T. vogelii* were obtained from the germplasm repository of the International Center for Tropical Agriculture (CIAT, Cali, Colombia). Seed of *T. candida* were provided by the Special-Purpose Legume Collection of the USDA–ARS, Griffin, GA. Seeds of *Tephrosia* spp. were planted in germination trays (December 2000) in a soilless potting mix (Metromix 500, Scotts, Marysville, OH) and transplanted at 3–4 wk of age to 20-liter pots containing sterile sand (Bonsal Play Sand, W. R. Bonsal Co., Charlotte, NC). One-yr-old seedlings of *Citrus macrophylla* Wester, used here as a susceptible control, were transplanted to 20-liter plastic pots containing sterile sand. All plants initially were grown in a glasshouse before infestation and subsequently maintained during the experimental period in an environmental chamber at a constant temperature of 26°C, 16:8 L:D. Maximum photosynthetic photon flux in the environmental chamber was 300 $\text{mol·s}^{-1}\text{·m}^{-2}$. Plants were watered weekly with a dilute fertilizer mix using water-soluble 20N-10P-20K at a rate of 150 mg·liter^{-1} N in double-distilled, deionized water. The pots were lined with a nylon mesh cloth to prevent escape of larvae through the drainage holes.

Insects. Diaprepes root weevils were obtained from a laboratory colony maintained by the U.S. Horticultural Research Laboratory, Ft. Pierce, FL. Larvae were reared on artificial diet according to Lapointe and Shapiro (1999). Larvae were weighed, placed in numbered plastic cups, and then randomly assigned to treatments. Teneral adults were placed in screened cages and provided fresh young foliage of *C. macrophylla* and water until selection for experiments. Healthy adults were selected and then randomly assigned to treatments.

Effect of *Tephrosia* spp. on Adult Feeding and Oviposition. Reproductively mature 1-mo-old adults were placed in 30 × 30 × 30-cm screened cages each containing bouquets consisting of fresh cut foliage of *C. macrophylla, T. vogelii,* or *T. candida* placed in vials containing water. An additional treatment consisted of adults caged without food (starvation control) but provided water (saturated dental wick). Cages contained strips (2 × 20 cm) of wax paper as oviposition substrates (Wolcott 1933). Five females and five males were placed in each cage and cages were placed in a glasshouse. Treatments were replicated three times for a total of 12 cages and 120 weevils. Bouquets were replaced daily with fresh foliage and examined for feeding for 11 d. Adult Diaprepes root weevils typically feed by notching the leaf margin. Feeding was measured by tracing the leaf area consumed (notching) during a feeding bout. Tracings of the total leaf area consumed per bouquet were digitally scanned and the resulting files were imported into an image analysis computer program (NIH Image, version 1.61; National Institutes of Health, http://rsb.info.nih.gov/nih-image/). The areas were then integrated to produce a measurement of leaf area consumed per bouquet per day. To assess oviposition, wax paper strips containing egg masses were removed and the bouquets were examined for eggs; the total number of eggs deposited was counted daily. Number of eggs per cage and leaf area consumed were analyzed by repeated measures analysis of variance (ANOVA) ($n = 3$) using the type III sum of squares for cage as the error term. Where appropriate, means were compared by Tukey's honestly significant differences (HSD) test (SAS Institute 1999).

Survival and Weight Gain of Larvae in No-Choice Pot Tests. Eight 20-liter plastic pots each of *T. vogelii, T. candida,* and *C. macrophylla* were moved into an environmental chamber at a constant 26°C on 16 April 2001. Three-wk-old larvae weighing between 50 and 100 mg were selected because neonate larvae or very early instars could escape the pots by crawling up the sides. Mean (±SEM) initial weight of larvae was 73.3 ± 0.8 mg ($n = 300$). Larvae at this stage of development (21–50 d after hatching at 26°C) have been shown to grow more quickly and presumably to ingest more than neonates or older larvae (Lapointe 2000). Five pots (replications) of each plant species were infested with 20 larvae each for a total of 300 larvae on 10 May 2001. Larvae were placed in pots by hand in holes made with a stick. Three pots of each species were left uninfested. At the time of infestation, all plants were ≈1 m tall. Weights of all larvae infesting the numbered pots were recorded to produce an initial mean larval weight for each pot. Larvae were recovered from the pots by careful sifting and examination of the plant roots and sand at 28 d after infestation. Larvae were weighed and weight gain was estimated by subtracting the mean initial larval weight for the corresponding pot. Weight gain and number of larvae recovered per pot were analyzed by one-way ANOVA and means were compared by Tukey's HSD test (SAS Institute 1999). The roots of uninfested plants were compared with those of infested plants to verify larval feeding damage.

Diet Incorporation Bioassays. Roots of *C. macrophylla, T. candida,* and *T. vogelii* were collected from potted plants grown in a greenhouse, lyophilized, ground in a blender and milled through a fine (30-mesh) screen. Experimental diets were prepared as per Lapointe and Shapiro (1999) except that root powder (Trials 1 and 2) or cellulose (Trial 3) were substituted proportionately for the dry diet components (citrus root weevil diet premix #1675 F, Bio-Serv, Inc., Frenchtown, NJ). In Trials 1 and 2, root powder was substituted at rates of 1.0/1.0, 0.5/1.5, and 0.1/1.9 g root powder per g premix per diet cup (PC100 one oz. cups and lids, Jet Plastica, Harrisburg, PA). The control consisted of diet cups containing diet without root powder (2 g dry diet premix per cup). The experimental diets were mixed with agar at 50–60°C and poured into polystyrene cups at ≈15 ml per cup. Larval Diaprepes root weevil were weighed and randomly assigned to each diet cup (one larva per cup) and kept in a dark incubator at 27°C for 31 d. Initial mean (±SEM) weight of larvae was 25.1 ± 0.5 mg. Diet cups were placed in trays and kept in sealed plastic bags. Larvae were removed and weighed at the end of 31 d or when they were observed to be dead. Because of a shortage of root powder of *T. vogelii,* Trial 1 was conducted with 10 larvae per treatment. Treatments consisted of three rates of root powder of either *T. vogelii, T. candida,* or *C. macrophylla* and a set of controls (diet only) for each species for a total of 120 larvae. Trial 2 was conducted to confirm the antibiotic effect of *T. candida.* Treatments consisted of three rates of root powder of *T. candida* or *C. macrophylla,* and diet-only controls. Sixty larvae were weighed and randomly assigned to each treatment including a diet-only control for a total of 420 larvae. The control larvae were divided into two groups of 30 larvae each. One group of 30 larvae were placed in each of the sealed plastic bags that contained either the *T. candida* or *C. macrophylla* treatments. Initial mean (±SEM) weight of larvae was 25.6 ± 0.3 mg.

The incorporation of root powder into artificial diet could have a negative effect on larval survival and weight gain because of antibiotic or antifeedant components present in the roots, or because of reduced nutritional value of the diet as a result of substitution. Therefore, we were interested to know the extent to which diet could be substituted by an inert filler without affecting larval growth or survival. A separate assay (Trial 3, Table 2) compared incorporation of cellulose (fibrous cellulose powder, cat. no. 4021 050, Whatman, Maidstone, England) at 0.01, 0.1, 1.0 and 2.0 g per diet cup. These rates correspond to 0.5, 5, 50, and 100% substitution of dry diet components. Thirty larvae were weighed and randomly assigned to each treatment including a diet-only control for a total of 150 larvae. Initial mean (±SEM) weight of larvae was 29.3 ± 0.6 mg. Mean weight gain of larvae in the diet incorporation bioassays was analyzed by one-way ANOVA and means were compared by Tukey's HSD test (SAS Institute 1999).

Table 1. Mean (±SEM) survival and weight gain of larval Diaprepes root weevil placed in pots containing plants of a citrus rootstock and two species of *Tephrosia* for 28 d

Species	% Survival[a]	Larval live wt (mg)		
		Initial	Final	Gain[b]
C. macrophylla	56.0 ± 11.5a	74.4 ± 1.4	150.4 ± 7.3	76.4 ± 7.3a
T. vogelii	73.0 ± 6.5a	72.8 ± 1.5	133.1 ± 6.5	60.4 ± 6.4a
T. candida	11.0 ± 2.5b	72.8 ± 1.4	69.4 ± 5.1	−4.1 ± 5.0b

Means followed by different letters are significantly different at $\alpha = 0.05$ by Tukey's HSD after a significant ANOVA.

[a] $F = 17.0$; df = 2, 12; $P < 0.01$.

[b] $F = 10.4$; df = 2, 12; $P < 0.01$.

Results

Effect of *Tephrosia* spp. on Adult Feeding and Oviposition. Egg production was similar in all cages, including the starvation control, until 5 d after infestation (Fig. 1A). Eggs produced during this period by starved females were likely the product of stored reserves from larval feeding. Therefore, oviposition was analyzed for days 5 through 11. For that period, there was a significant effect of plant species ($F = 17.9$; df = 3,8; $P < 0.01$). Very few eggs (5 ± 5) were laid by starved females after day 5. From day 5 to day 11, there was no significant difference in mean (± SEM) total oviposition between adults caged with *C. macrophylla* (2,317 ± 389) or *T. vogelii* (2,178 ± 282); oviposition

Table 2. Effect of substitution of artificial diet by lyophilized root powder of two species of *Tephrosia* or *Citrus macrophylla*, or by cellulose on mean (±SEM) weight gain and survival of larvae of the Diaprepes root weevil

Diet amendment	% Substitution	n	Wt gain (mg)	Survival (%)
Trial 1				
Control	0	10	387.3 ± 94.3a	100
C. macrophylla	5	10	313.6 ± 34.8a	90
C. macrophylla	25	10	328.7 ± 49.9a	90
C. macrophylla	50	10	341.2 ± 33.2a	100
Control	0	10	316.7 ± 47.9a	100
T. vogelii	5	10	306.9 ± 37.5a	100
T. vogelii	25	10	316.5 ± 54.6a	90
T. vogelii	50	10	318.1 ± 26.1a	100
Control	0	10	341.6 ± 55.2a	100
T. candida	5	10	180.2 ± 47.5ab	70
T. candida	25	10	121.3 ± 44.0ab	60
T. candida	50	10	59.2 ± 42.8b	30
Trial 2				
Control	0	30	462.4 ± 17.8a	97
C. macrophylla	5	60	427.5 ± 16.2ab	95
C. macrophylla	25	60	363.7 ± 19.9c	98
C. macrophylla	50	60	374.8 ± 10.9bc	98
Control	0	30	431.3 ± 34.3a	100
T. candida	5	60	297.0 ± 24.1b	95
T. candida	25	60	120.5 ± 29.9c	42
T. candida	50	60	43.5 ± 15.6c	32
Trial 3				
Control	0	30	533.7 ± 17.0a	100
Cellulose	0.5	30	486.2 ± 18.7ab	97
Cellulose	5	30	493.1 ± 17.3ab	100
Cellulose	50	30	451.9 ± 13.7b	97
Cellulose only	100	30	−7.5 ± 0.8c	97

Means within trials and within species for Trials 1 and 2 followed by different letters are significantly different at $\alpha = 0.05$ by Tukey's HSD after a significant ANOVA.

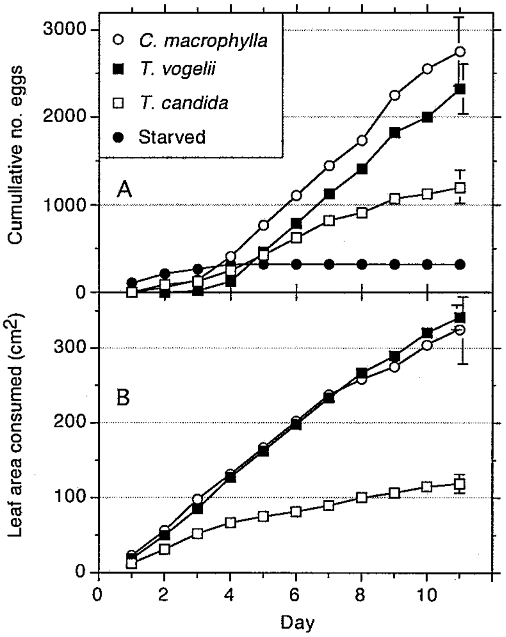

Fig. 1. Mean cumulative oviposition (A) and cumulative leaf area consumed (B) by adult Diaprepes root weevils provided fresh foliage of *C. macrophylla*, *T. candida*, or *T. vogelii* in a no-choice cage bioassay. Error bars are SEM (n = 5).

of adults caged with *T. candida* (953 ± 191) was significantly reduced to 41% of that on *C. macrophylla* (Tukey's HSD).

There was a significant effect of plant species on adult leaf consumption when adults were caged for 11 d on foliage of *C. macrophylla*, *T. candida*, or *T. vogelii* (ANOVA, $F = 18.8$, df = 2, 6, $P < 0.01$). There was no significant difference in leaf area consumed by adults caged with foliage of *C. macrophylla* or *T. vogelii*. Consumption of *T. candida* was significantly reduced compared with *C. macrophylla* or *T. vogelii* (Tukey's HSD, $\alpha = 0.05$). Adults caged with *T. candida* consumed a total (mean area consumed per cage) of 117.5 ± 12.5 cm^2 compared with 322.9 ± 45.2 and 340.8 ± 16.0 cm^2 of *C. macrophylla* and *T. vogelii*, respectively (Fig. 1B).

Survival and Weight Gain of Larvae in No-Choice Pot Tests. Fewer larvae survived the period of infestation in pots containing *T. candida* compared with larvae in pots containing *T. vogelii* or *C. macrophylla* (Table 1). Those larvae that survived the period of infestation in pots containing *T. candida* lost weight on average compared with their initial weights (Table 1). There was no significant difference in weight gain of larvae reared in pots containing *T. vogelii* or *C. macrophylla*. Weight gain of larvae in pots with either *T. vogelii* or *C. macrophylla* was significantly greater than weight gain of larvae in pots with *T. candida*. We examined the roots at the end of the period of infestation and observed feeding damage on all of the infested plants, including *T. candida*.

Diet Incorporation Bioassays. In Trial 1, there was no effect of increasing substitution of diet by root powder of *C. macrophylla* or *T. vogelii* on survival or weight gain of larvae (Table 2). Larval survival was high and weight gain exceeded 300 mg for all rates of root powder incorporation of *C. macrophylla* or *T. vogelii*. Increasing substitution of diet by root powder of *T. candida* resulted in increased larval mortality and decreased weight gain. In Trial 2, all rates of incorporation of root powder of *T. candida* resulted in reduced weight gain compared with the diet-only control (Table 2). As in Trial 1, survival of larvae and weight gain decreased with increasing concentration of root powder. Nearly all larvae reared on pure cellulose survived although they lost weight. Larvae reared on diet with 50% substitution of diet by cellulose gained a mean (±SEM) of 451.9 ± 13.7 mg, only slightly less than the diet-only control (533.7 ± 17.0 mg).

Discussion

To our knowledge, there are but two cursory references (Fennah 1938, 1942) to the allelochemical properties of *T. candida* toward the Diaprepes root weevil. Fennah's observations appear to have been well-founded, although we have not found a description of his methods. In the studies reported here, adults were deterred from feeding and produced proportionately fewer eggs when caged with foliage of *T. candida* compared with foliage of its congener, *T. vogelii* or *C. macrophylla*. It appears that the leaves of *T. candida*, but not those of *T. vogelii*, contain an antifeedant(s) with activity toward adult Diaprepes root weevil. We observed feeding damage by larvae on roots of both *Tephrosia* species, but weight gain and survival of larvae placed in pots containing *T. candida* were greatly reduced, whereas larvae placed in pots containing *T. vogelii* survived and gained weight at a rate equivalent to larvae placed in pots containing *C. macrophylla* (Table 1). This evidence suggests that larvae were not deterred from feeding on *T. candida* but were intoxicated by ingesting its roots. Larvae can survive long periods in soil without food given adequate soil moisture (Lapointe and Shapiro 1999). Low survival of larvae in pots with *T. candida* and evident feeding damage on roots of *T. candida* indicate the involvement of a toxicant, but not an antifeedant for larval Diaprepes root weevil. This would be an ideal combination of properties for a companion or cover crop.

The diet incorporation assays demonstrated increasing mortality and decreasing weight gain with increasing concentration of lyophilized root of *T. candida* in the artificial diet compared with diet-only controls and to diet containing root powder of a susceptible citrus rootstock, *C. macrophylla*. This effect was not observed with root powder of *T. vogelii*. Also, substitution of diet by cellulose showed that even when diet is diluted with a nutritionally inert filler, larvae are capable of surviving and gaining weight. When placed on a diet of pure cellulose, larval survival was 100% even though the larvae lost weight (Table 2). Therefore, decreased survival and weight gain by larvae fed diet containing *T. candida* were the result of ingestion of a toxicant and not deterrence from feeding. This confirmed observations that larvae of *D. abbreviatus* survive long periods (weeks) of starvation without significant mortality.

Tephrosia species contain complex mixtures of rotenoids and other flavonoids (Irvine and Freyre 1959, Gómez-Garibay et al. 2002). *T. candida* has been shown to contain phytochemicals that may have insecticidal or antifeedant properties (Kole et al. 1992; Andrei et al. 1997, 2002). Our results indicate that the phytochemicals responsible for the antifeedant and toxic properties of *T. candida* toward *D. abbreviatus* are not shared by *T. vogelii.* For this reason, compounds such as rotenone, tephrosin, and deguelin, all present in *T. vogelii* (Gaskins et al. 1972) may not be toxic to *D. abbreviatus* at concentrations found in the roots. Data from our laboratory indicate a very low dermal toxicity of rotenone toward larvae (S.L.L., unpublished data) as was noted by Simanton and Bullock (1973). Preliminary analyses of extracts of roots of *T. candida* indicate the presence of a complex of flavonoids including rotenone. The diet incorporation assay described here will now be used to identify specific compounds or combinations that confer toxic and antifeedant properties to roots of *T. candida* against the Diaprepes root weevil. It remains to be seen whether *T. candida* can be used as a cover or mulch in crops susceptible to this weevil or if it will be possible to use the compounds responsible for the effects demonstrated here for commercial production systems. In light of the wide host range of *D. abbreviatus* (Simpson et al. 1996) and the low level of resistance present within sexually compatible species of citrus (Lapointe and Bowman 2002, Lapointe et al. 1999), we are encouraged to pursue the biochemical basis of the toxic compounds in *T. candida* for their potential as a component of a control strategy for *D. abbreviatus* in citrus.

Acknowledgments

We thank Anna Sara Hill, Laura Hunnicutt, Dina Grayson, and Kathy Moulton (USDA–ARS, Ft. Pierce, FL) for technical assistance with glasshouse bioassays. Brad Morris (USDA–ARS, Griffin, GA), and Daniel DeBouck (CIAT, Cali, Colombia) kindly provided botanical seed of *Tephrosia* spp. Supported in part by a grant from the Florida Citrus Production Research and Advisory Council.

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Received for publication 30 October 2002; accepted 31 January 2003.