Biology and Host Range of *Tecmessa elegans* (Lepidoptera: Notodontidae), a Leaf-Feeding Moth Evaluated as a Potential Biological Control Agent for *Schinus terebinthifolius* (Sapindales: Anacardiaceae) in the United States

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ABSTRACT During surveys for natural enemies that could be used as classical biological control agents of *Schinus terebinthifolius* Raddi (Brazilian pepper), the caterpillar, *Tecmessa elegans* Schaus (Lepidoptera: Notodontidae), was recorded feeding on the leaves of the shrub in South America. The biology and larval and adult host range of this species were examined to determine the insect's suitability for biological control of this invasive weed in North America and Hawaii. Biological observations indicate that the larvae have five instars. When disturbed, the late instar larvae emit formic acid from a prothoracic gland that may protect larvae from generalist predators. Larval host range tests conducted both in South and North America indicated that this species feeds and completes development primarily on members of the Anacardiaceae within the tribe Rhoeae. Oviposition tests indicated that when given a choice in large cages the adults will select the target weed over *Pistacia* spp. However, considering the many valued plant species in its host range, especially several North American natives, this species will not be considered further for biological control of *S. terebinthifolius* in North America.

KEY WORDS Brazilian pepper, weed biological control, exocrine gland, host specificity testing

Brazilian peppertree (*Schinus terebinthifolius* Raddi, Anacardiaceae) is a perennial shrub native to Argentina, Brazil, Paraguay and Uruguay (Barkley 1944, 1957; Muñoz 2000; F. M., unpublished data). This species has been introduced into many countries around the world as an ornamental and has successfully naturalized in sub-tropical areas (15–30°) of both the northern and southern hemispheres (Morton 1978, Ewel 1986, Panetta and McKee 1997). Currently, Brazilian peppertree is listed as a prohibited plant and a noxious weed in Florida, and is considered an invasive species in Florida, California, Texas, and Hawaii (Randall 2000, Hawaii State Alien Species Coordinator [HSASC] 2001, Florida Exotic Pest Plant Council [FLEPPC] 2005, U.S. Department of Agriculture-Natural Resources Conservation Service [USDA-NRCS] 2009). In its exotic range the tree decreases the biodiversity of infested natural areas by aggressively invading a variety of coastal and upland habitats (Mytinger and Williamson 1987, Gann et al. 2001). In Florida, infestations of *S. terebinthifolius* are estimated to occupy over 283,400 ha (Ferriter and Pernas 2005). Brazilian peppertree constitutes not only a threat to natural areas but also to agriculture and cattle production in Florida and Hawaii (Morton 1978, Ewel 1986, Yoshioka and Markin 1991). This species produces allelopathic compounds that suppress the growth of other plant species (Gogue et al. 1974, Morgan and Overholt 2005) and is also suspected of causing allergic reactions and respiratory illness in sensitive humans from volatiles released by the leaves, flowers, and fruits (Morton 1978).

Biological control efforts of Brazilian peppertree began in Hawaii in the 1950s and resulted in the release of three insect species: a gall-forming caterpillar, *Crasimorpha infuscata* Hodges (Lepidoptera: Gelechiidae), a leaf-tying caterpillar, *Episimus unguiculus* Clarke (=*E. utilis* Zimmerman) (Lepidoptera: Tortricidae), and a seed-feeding beetle, *Lithraeus atronotatus* (Pic) (Coleoptera: Bruchidae) (Davis and Krauss 1962; Krauss 1962, 1963; Hight et al. 2002). Only the last two species established field populations in Hawaii, but they are exerting only negligible control of the weed population (Hight et al. 2002).

Exploration in South America for potential natural enemies for the classical biological control of Brazilian peppertree in Florida conducted in the 1980s and 1990s revealed the presence of at least 200 species of natural enemies (Bennett et al. 1990, Bennett and Habeck 1991). Three insects were selected for further studies: the leaf-feeding sawfly *Heteroperreyia hubrichi* Malaise (Hymenoptera: Pergidae), the sap-sucking thrips *Pseudophilothrips ichini* Hood (Thysanoptera:

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Phlaeothripidae), and the defoliating caterpillar *E. unguiculus* (Medal et al. 1999, Hight et al. 2002, Martin et al. 2004). To date, none of these biological control candidates have been released in the continental United States. The continuous spread of invasive Brazilian peppertree and the environmental concerns regarding pesticide exposure motivated the search for natural enemies that are safe biological control agents against this weed.

Recent genetic characterization of Brazilian pepper using chloroplast DNA revealed the presence of eleven haplotypes in South America (haplotypes A, C-J), only two of which occur in Florida (haplotypes A, B, and intraspecific hybrids) (Williams et al. 2005). Apparently, not all these haplotypes have the same nutritional value or attractiveness to specialized herbivore species. Comparative insect feeding and survival trials with two thrips species indicated that different host haplotypes may be more acceptable and nutritious (Manrique et al. 2008). Other insects being developed for biological control may be similarly restricted to particular haplotypes and thus these results are relevant to our testing of potential biological control agents of *S. terebinthifolius.*

During explorations conducted in northern Argentina and Brazil between 2006 and 2010, the leaf-feeding moth *Tecmessa elegans* Schaus (Lepidoptera: Notodontidae), was recorded as damaging to *S. terebinthifolius* and identified as a candidate for further investigations (Mc Kay et al. 2009, G.S.W. et al., unpublished data). Four species of *Tecmessa* have been described, namely, *T. annulipes* Berg, *T. cerurata* Dognin, *T. elegans*, and *T. phyllis* Druce (Pastrana 2004, BayScience Foundation INC. 2004–2008, Beccaloni et al. 2003). However, host records are available for only two species: *T. annulipes* recorded on *Lithrea brasiliensis* Marchant, *Schinus molle* L., and *Salix* sp. (Salicaceae) in Argentina (Pastrana 2004) and *T. elegans* on *L. brasiliensis*, *Lithrea* sp., *S. terebinthifolius*, and *S. weinmannifolius* Engl. in Argentina (Pastrana 2004, Mc Kay et al. 2009) and *Lithrea* sp. ("aroeira") (D'Araujo et al. 1968, Pastrana 2004) and *S. terebinthifolius* (G.S.W., unpublished data) in Brazil.

Many Notodontidae larvae have an exocrine gland opening in the ventral portion of the first prothoracic segment of the fourth and fifth instars (Weatherston et al. 1986, Godfrey and Appleby 1987, Markin et al. 1989). These glands have been shown to emit defensive compounds that protect the caterpillar from predators (Eisner et al. 1972). The presence of such a potentially antipredator defense could provide protection to larvae from generalist natural enemies and facilitate establishment of this biological control agent after release (Wheeler et al. 2002).

In view of the limitations of existing control methods for Brazilian pepper and its continued spread, we conducted additional biology and host specificity studies, both in South and North America, to determine the actual suitability of *T. elegans* as a biological control agent in the United States.

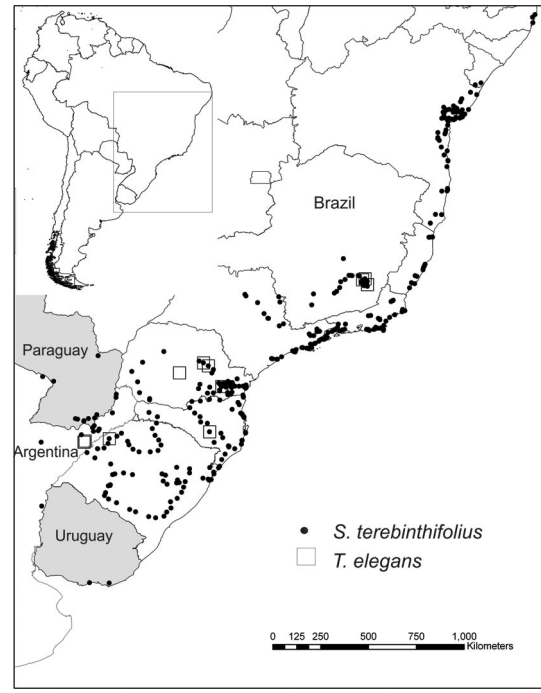

Fig. 1. Map of the distribution of *S. terebinthifolius* in South America. Small black dots represent sites where host plant *S. terebinthifolius* was sampled and open boxes represent sites where *T. elegans* was found during surveys from 2006 to 2009.

Materials and Methods

Distribution of *T. elegans* in South America. The distribution of *T. elegans* was determined by periodic surveys conducted generally for biological control agents throughout the range of the host, Brazilian pepper. The plant is distributed from Natal, Rio Grande Do Norte, Brazil (S5.78975 W35.20858) to Concordia, Entre Rios, Argentina (S31.35089 W58.09275) (G.S.W. et al., unpublished data). When found, cultures of *T. elegans* were established at laboratories in Argentina and the USA from eggs and larvae collected on *S. terebinthifolius* between 2006 and 2009 in Argentina and Brazil, respectively (Fig. 1).

Biology of *T. elegans.* Forty newly hatched larvae were reared individually in 0.7-liter plastic jars with perforated lids and moist tissue paper containing bouquets of freshly excised leaves. Leaf petioles of *S. terebinthifolius* were inserted in small floral tubes filled with water. Bouquets were replaced every 48 h. Head capsule widths were measured with a stereo microscope (40×) to determine the number and the duration of larval instars. The duration of the pupal stage was also recorded. Adult longevity and fecundity were estimated from 13 pairs of newly emerged *T. elegans.* Each pair was placed in a 3-liter ventilated plastic container and reared as above. A replicate was terminated when the female died; males were replaced if they died before the female. For each pair, we recorded preoviposition period, number of eggs laid and

longevity of females. All experiments were conducted in controlled environment chambers at 25 ± 1°C and 60 ± 5% RH, with a 14:10 (L:D) photoperiod unless described otherwise.

Defensive Gland. Microscopic examination of all larval instars was conducted searching for an exocrine gland opening. Once found, the analysis of the gland contents was conducted with ^{13}C nuclear magnetic resonance (NMR) spectrum measured on a Brüker AC-200 NMR spectrometer; 10% deuterium oxide served as the solvent.

Host Range of *T. elegans*

The host range of *T. elegans* was determined with no-choice larval survival tests (Argentinean and North American tests) and adult no-choice and multiple-choice oviposition tests. Experiments were performed on native South American, agricultural, and ornamental species at the USDA-ARS-SABCL in Hurlingham, Argentina (see Tests Conducted in Argentina below). Additionally, no-choice larval survival tests were performed on native North American, Hawaiian, and Caribbean species and agricultural species at the USDA-ARS-IPRL in Ft. Lauderdale, FL (see Tests Conducted in North America below).

Tests Conducted in Argentina. Ten plant species in six South American Anacardiaceae genera were selected based on taxonomic relatedness to *S. terebinthifolius*, economic importance, and availability, as follows: *Schinus terebinthifolius* haplotype D from Argentina and haplotype B from Florida (commercially available in Argentina) (Williams et al. 2005, G.S.W., unpublished data), *S. areira* L. (aguaribay), *S. lentiscifolius* Marchand (Caroba), *S. molle* L. (Peruvian peppertree), *Astronium balansae* Engl. (urunday), *Lithrea molleoides* (Vell.) Engl (aroeira blanca), *Schinopsis balansae* Engl. (quebracho), and the agricultural species *Pistacia integerrima* J.L. Stewart ex Brandis, *P. vera* L. (pistachio nut) (all from the tribe Rhoeae), and *Mangifera indica* L. (Mango) (tribe Anacardieae) (Mitchell and Mori 1987). Special attention was given to *Pistacia* spp., important crops in the western United States. Test plants also included three South American species of Sapindaceae: *Cardiospermum grandiflorum* Swartz (showy balloonvine), *Sapindus saponaria* L. (wingleaf soapberry; also native to North America) and *Serjania glabrata* Kunth. These are closely allied to the Anacardiaceae within the order Sapindales (Gadek et al. 1996, Pell 2004, APG III 2009). All plants were grown in 3 liter pots containing potting soil. No fertilizers or pesticides were applied to these plants.

No-Choice Larval Survival and Growth Tests. In each replicate, five newly emerged larvae were placed in 0.7-liter plastic containers and fed freshly excised leaves as described above (see Biology of *Tecmessa elegans*). Prepupae were transferred to 0.5-liter plastic jars containing a layer of moist peat moss for pupation. These jars were kept under the same controlled conditions until adult emergence. We recorded the proportion of larvae that survived the first 72 h of testing, the development time to pupation and the number of adults that emerged for each test plant.

Fecundity and No-Choice Oviposition Tests. Fecundity and no-choice oviposition of *T. elegans* were assessed on *S. terebinthifolius* (haplotype B), *P. vera* and *P. integerrima.* In each replicate, one pair of newly emerged adults was placed in a 3-liter plastic container and provided freshly excised bouquets of each species as described above (see Biology of *Tecmessa elegans*). A replicate was ended when the female died; if the male died first it was replaced. We recorded the number of eggs laid on leaves.

Multiple-Choice Oviposition Test. The oviposition preference of *T. elegans* was evaluated for the entire duration of the adult lifespan (≈7 d) in an outdoor walk-in screen cage (3 × 6 × 2 m). The plants had not been used in previous tests and included: *S. terebinthifolius* (haplotype D), *P. vera*, and *P. integerrima.* Eight potted plants of each species (1.5–2 m high) with similar foliar area were randomly arranged inside the cage. Twenty four adults were released in the center of the cage. The number of eggs and the location of eggs and adults were recorded daily at 10 a.m. This test was replicated three times with fresh adults.

Tests Conducted in North America. Plants were grown in a research garden and fertilized with both liquid (Miracle-Gro for acid loving plants, 30N-10P-10K) and slow-release (Multicote 4, 14N-14P-16K) formulations according to label directions. No pesticides were applied within 3 mo of the beginning of these experiments. Just before feeding to larvae, leaves were clipped from plants and dipped in a 2% bleach solution for 60 s to reduce larval exposure to disease organisms. This treatment was immediately followed by two tap-water rinses to remove residual bleach. Plant species included the North American Anacardiaceae species *Metopium toxiferum* (L.) Krug & Urb. (Florida poisontree), *Toxicodendron radicans* (L.) Kuntz (eastern poison ivy), *Cotinus obovatus* Raf. (American smoketree), *Rhus copallinum* L. (winged sumac), *Malosma laurina* (Nutt.) Nutt. Ex Abrams (laurel sumac), the Hawaiian species *Rhus sandwicensis* A. Gray, the Caribbean species *Comocladia dodonaea* (L.) Urb. (poison ash) (all Rhoeae tribe), *Spondias mombin* L (yellow mombin), *S. purpurea* L. (purple mombin) (tribe Spondiadeae), and the agricultural species, *Anacardium occidentale* L. (Cashew) (Anacardieae tribe) (Mitchell and Mori 1987). A culture was established from *T. elegans* larvae collected during the February 2009 survey in Campo Largo, Paraná, Brazil. These larvae were introduced under quarantine at the USDA-ARS-IPRL and reared to the adult stage on Florida Brazilian pepper leaves (haplotypes A and B). Once the first instars from the F_1 generation hatched, they were briefly (<24 h) allowed to feed on Brazilian pepper leaves on which the eggs were laid before assignment to specific plant treatments. The neonates transferred without assistance onto new test leaves in plastic vented boxes (13 × 3 cm height). These containers were positioned in a greenhouse (28 ± 5°C), under ambient photoperiod, and lightly misted daily to add humidity. Each

container was lined with filter paper that was replaced as needed.

No-Choice Larval Survival and Growth Rate. The experimental larvae were fed excised leaves from different test plant species in no-choice studies. The tests were replicated with 25 larvae for *T. radicans*, *S. mombin*, and *S. purpurea*, and with 10 larvae for all other plant species. All leaves were changed every 2–3 d. Each larva was reared individually in vented boxes (13 × 3 cm height). As the larvae stopped feeding and turned a pink color, extra paper towels were added as a pupation substrate. Data were collected on survival at the 4 d larval stage, survival to the adult stage, and development time to the pupal and adult stages. Additionally, the pupae were sexed and weighed (±0.1 mg; Ohaus E10640) at 14 d.

Statistical Analysis. Data from the Argentinean tests were analyzed with statistical package Statistica (StatSoft. Inc., 1984–2000). For the biology studies, the mortality of each life stage was compared using the Fisher exact test (Zar 1996). For the larval no-choice trials, the proportion of dead larvae after 72 h were compared using a Kruskal-Wallis test with multiple comparisons (Conover 1999). The proportion of emerged adults for each test plant was compared using a one-way analysis of variance (ANOVA). Before analysis the data were square root-arcsine transformed to comply with the assumptions of the ANOVA. Means were compared using Tukey's honestly significant difference (HSD) for unbalanced designs (Zar 1996). The larval stage duration was compared using a Kruskal-Wallis test with multiple comparisons. In the adult no-choice oviposition tests, all the variables recorded were analyzed using a Kruskal-Wallis test. The number of eggs was transformed (Log_{10} +1) before analysis to comply with the assumption of homogeneity of variance. Data from the North American no-choice tests were analyzed with SAS (SAS Institute 1990). The larval, pupal, and adult survival results from the tests of North American, Hawaiian, and Caribbean plants were analyzed with χ^2 tests. Pupal weights and development times were each analyzed with one-way ANOVAs using plant species as the main effect. In all ANOVAs, means were compared with a Tukey's HSD ($P < 0.05$).

Results

Distribution of *T. elegans* in South America. General surveys conducted for biological control agents of *S. terebinthifolius* found that *T. elegans* was restricted to the more southern region as it was never collected north of Minas Gerais, Brazil (Fig. 1). In Argentina, *T. elegans* was found at seven sites in the northeastern provinces of Corrientes and Misiones on *S. terebinthifolius* and *S. weinmannifolius* (Mc Kay et al. 2009); in Brazil, it was found near Viçosa, Minas Gerais, Castro, and Campo Largo, Paraná, on *S. terebinthifolius* and *L. brasiliensis* (G.S.W. and F.M., unpublished data). Eggs and larvae of *T. elegans* were present in the field from December to April.

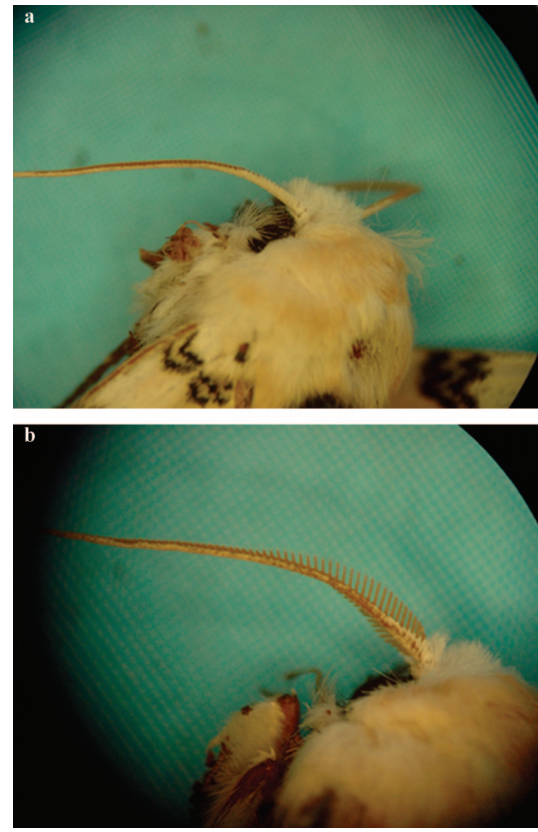

Fig. 2. Sexually dimorphic antennae of *T. elegans* adults: (a) female simple antenna; (b) male pectinate antenna. (Online figure in color.)

Biology of *T. elegans*. Adults (wingspan: 3 cm) are creamy white in color with three sinuous narrow dark lines across each forewing. The antennae are sexually dimorphic, pectinate in males and simple in females (Fig. 2). Females laid 90.2 ± 75.7 (mean ± SD) chalky, hemispherical eggs (0.96 ± 0.03 mm diameter) in compact clusters of varying number (10–80 eggs) generally on the lower leaf surface, after a 2 ± 1 d preoviposition period. Egg incubation period was ≈12 d. Larvae of *T. elegans* completed five instars distinguished by distinct head capsule widths (Table 1). Each successive instar head capsule width was generally 1.6×-fold larger than the previous instar and ranged from 0.55 to 3.35 mm. Neonates fed gregariously skeletonising the leaf blade usually on the lower surface. As larvae develop, they eat most of the leaf except for the larger veins. When at rest, the larvae hold their last four abdominal segments in an elevated position. Body color changed progressively from burgundy in the early instars to alternate yellow and burgundy rings in the latter instars.

When the larvae reached the fifth instar, they dispersed throughout the plant and fed solitarily. The larval stage lasted 22.7 ± 0.8 d (Table 1). Total mortality in the larval stage was 40%, being higher during the fifth instar (Table 1). Mature larvae spun a debris-

Table 1. Life stage duration, mortality, and larval head capsule widths of *T. elegans* fed *S. terebinthifolius*

Life stage	*n*	Life stage duration (d)		No. of dead individuals in each stage[a]	Head capsule width (mm)	
		Mean ± SD	Range		Mean ± SD	Range
L I	40	4.1 ± 0.6	4–5	1[a]	0.55 ± 0.01	0.54–0.59
L II	39	3.9 ± 0.6	3–5	4[a]	0.84 ± 0.02	0.78–0.87
L III	35	4.0 ± 0.9	3–5	5[ab]	1.34 ± 0.06	1.12–1.44
L IV	30	3.7 ± 0.7	3–5	0[ab]	2.10 ± 0.08	1.90–2.22
L V	30	7.3 ± 1.2	5–9	6[c]	3.35 ± 0.26	3.17–3.83
Pupa (cocoon)	24	29.0 ± 5.7	24–45	2[a]		

[a] Total no. dead individuals compared by Fisher's exact test (2 × 2 Tables); those followed by the same letter are not significantly different ($P > 0.05$).

encrusted cocoon buried a few centimeters in soil where they pupated. Male and female pupae differed in the position and distance of the anus and genital orifices (Fig. 3). The time between cocoon formation and adult emergence was 29.0 ± 5.7 d (Table 1).

Defensive Gland. An exocrine gland opening was located on the ventral portion of the first prothoracic segment of fourth and fifth instar larvae (Fig. 4). The larvae responded when disturbed with sudden movements and emitted a fine spray that had a range of ca. 10 cm. Analysis of the gland contents revealed only the presence of formic acid.

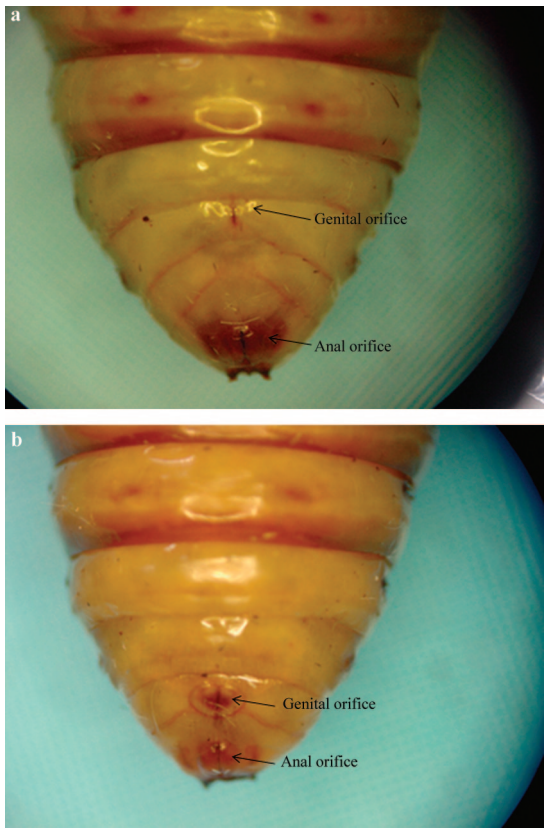

Fig. 3. Differences in the position of the anal and genital orifices of *T. elegans* pupae: (a) female pupa; (b) male pupa. (Online figure in color.)

Host Range of *T. elegans*

No-Choice Larval Survival and Growth Tests: Argentina. *T. elegans* showed a wide host range within the tested Anacardiaceae species (Table 2). Although larval mortality and duration of the larval stage varied significantly among test plants, adult emergence was recorded on all of the South American Anacardiaceae and also on the economically important *Pistacia* species. However *T elegans* larvae did not survive >24–48 h when fed the economic species *M. indica* nor did they survive on the Sapindaceae species *C. grandiflorum*, *S. glabrata*, or *S. saponaria.*

No-Choice Larval Survival and Growth Tests: North America. As with the tests conducted in Argentina, similar tests on *T. elegans* in the United States showed a broad host range. Complete larval development occurred on all plants except the two *Spondias* spp. and *T. radicans.* Relatively low survival occurred with larvae fed the Caribbean *C. dodonaea* and the Hawaiian species *R. sandwicensis* (Table 3). Additionally, development time to pupal and adult stages were generally longer on these same species, *C. dodonaea* and *R. sandwicensis.* Pupal weights were significantly higher for females (548.9 ± 16.2 mg) compared with males (413.2 ± 13.0 mg; $F_{1,48} = 60.26$; $P < 0.0001$). In addition, pupal weights were greatest for larvae fed *S. terebinthifolius* and *R. copallinum* compared with those fed *C. obovatus*, *C. dodonaea*, and *R. sandwicensis.* Insect gender did not influence pupal or adult developmental time.

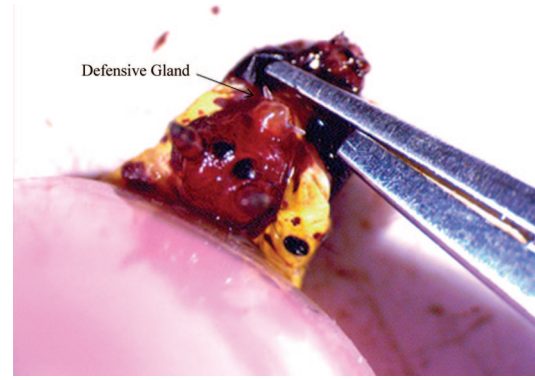

Fig. 4. Ventral prothoracic gland of *T. elegans* larvae. (Online figure in color.)

Table 2. No-choice larval survival, development time test of *T. elegans* in Argentina

Test plant family/species	Number of replications	Proportion of surviving larvae within 72 h[a]	Larval duration to pupa (d) (Mean ± SD)[b]	Proportion survival to the adult (Mean ± SD)[c]
Anacardiaceae				
Schinus terebinthifolius haplotype D	11	0.76 ± 0.15[c]	23.6 ± 2.2[ab]	0.44 ± 0.23[c]
Schinus terebinthifolius haplotype B	11	0.91 ± 0.13[abc]	22.0 ± 1.1[a]	0.42 ± 0.24[c]
Astronium balansae	10	0.68 ± 0.33[c]	25.4 ± 1.9[bcd]	0.06 ± 0.09[ab]
Lithrea molleoides	10	0.68 ± 0.47[abc]	31.7 ± 5.5[de]	0.22 ± 0.22[abc]
Mangifera indica	10	0	—	0
Pistacia integerrima	10	0.8 ± 0.33[abc]	34	0.02 ± 0.06[a]
Pistacia vera	10	0.84 ± 0.16[bc]	25.1 ± 2.8[bc]	0.26 ± 0.28[abc]
Schinus areira	10	0.96 ± 0.08[ab]	27.9 ± 1.4[cde]	0.26 ± 0.28[bc]
Schinus lentiscifolius	10	0.92 ± 0.19[ab]	33.3 ± 3.7[e]	0.18 ± 0.18[abc]
Schinus molle	10	0.9 ± 0.17[abc]	22.2 ± 1.2[ab]	0.42 ± 0.29[c]
Schinopsis balansae	10	1[a]	33.9 ± 3.5[e]	0.16 ± 0.18[abc]
Sapindaceae				
Cardiospermum grandiflorum	10	0	—	0
Sapindus saponaria	5	0	—	0
Serjania glabrata	10	0	—	0

Means within a column followed by different letters are significantly different ($P < 0.05$).

[a] Proportion of surviving larvae during first 72 h: Kruskal-Wallis test ($H_{(N: 102;\ df: 9)} = 18.39$; $P < 0.01$); *M. indica* and Sapindaceae species were not included in the analysis.

[b] Larval duration to pupa: Kruskal-Wallis test ($H_{(N: 76;\ df: 8)} = 60.27$; $P < 0.0001$); *P. integerrima*, *M. indica*, and Sapindaceae species were not included in the analysis as few or no larvae pupated on these species.

[c] Proportion survival to adult: One-way ANOVA: $F_{(9, 92)} = 5.47$; $P < 0.0001$); *M. indica* and Sapindaceae species were not included in the analysis.

Fecundity and No-Choice Oviposition Tests. The average number of eggs laid on leaves was higher on *S. terebinthifolius* than the other test species, however, a considerable number of eggs were found on *P. integerrima* and relatively few on *P. vera* (Table 4). Despite large differences, variation in oviposition was very high and significant differences were only found between *P. vera* and the other two species (Table 4).

Multiple-Choice Oviposition Tests. When offered a choice, females of *T. elegans* showed a clear oviposition preference for *S. terebinthifolius* (Table 5). In the large cage, eggs were only found on plants of this species and on the walls of the cage. In the first replicate, eggs were only laid on the cage walls. In addition, visual observations indicated that adults were only found on *S. terebinthifolius* plants and on the walls of the cage.

Discussion

The laboratory results presented here showed that *T. elegans* larvae fed and completed development on many valued plant species from South and North America, Hawaii, and the Caribbean. This is in contrast to previous indications of *T. elegans* as a potential biological control candidate against *S. terebinthifolius* in the United States. Available records from the literature, Lepidoptera host-plant database (Pastrana 2004, Robinson et al. 2009) and field host data obtained

Table 3. Results (mean ± SE) of neonate *T. elegans* feeding, survival, development time, and pupal weights on excised leaves of different test plant species in United States

Test plant species	Total larvae	Larval feeding	No. larvae[a] surviving after 4 d	No. pupae surviving[b]	Developing time (d) to pupa[c]	Pupal wt (mg)[d]	No. adult surviving[e]	Developing time (d) to adult[f]
Schinus terebinthifolius	10	Y	10	10	24.2 ± 0.3[c]	530.9 ± 27.0[a]	10	52.9 ± 0.9[b]
Metopium toxiferum	10	Y	10	7	24.3 ± 0.4[bc]	440.3 ± 23.2[abc]	7	52.9 ± 1.1[b]
Toxicodendron radicans[g]	25	Y	0	0	—	—	0	—
Anacardium occidentale	10	Y	7	6	24.5 ± 0.6[bc]	469.9 ± 49.4[abc]	6	52.7 ± 1.1[b]
Spondias mombin[g]	25	Y	0	0	—	—	0	—
Spondias purpurea[g]	25	Y	0	0	—	—	0	—
Cotinus obovatus	10	Y	10	8	24.8 ± 0.6[bc]	405.0 ± 26.5[b]	8	53.3 ± 0.8[b]
Comocladia dodonaea	10	Y	7	4	34.0 ± 3.4[a]	345.8 ± 15.7[c]	4	60.0 ± 3.3[a]
Rhus copallinum	10	Y	10	10	23.7 ± 0.7[c]	543.3 ± 24.5[a]	10	50.6 ± 0.8[b]
Rhus sandwicensis	10	Y	5	5	28.4 ± 0.9[b]	365.8 ± 32.8[b]	5	55.8 ± 1.3[ab]
Malosma laurina	10	Y	9	7	24.9 ± 0.4[bc]	510.7 ± 29.3[ab]	6	53.3 ± 1.2[b]

[a] $\chi^2_{10} = 124.1$; $P < 0.0001$.

[b] $\chi^2_{10} = 96.9$; $P < 0.0001$.

[c] One-way ANOVA: $F_{(7,49)} = 11.19$; $P < 0.0001$. Means followed by different letters are significantly different ($P < 0.05$).

[d] One-way ANOVA: $F_{(7,49)} = 5.73$; $P < 0.0001$. Means followed by different letters are significantly different ($P < 0.05$).

[e] $\chi^2_{10} = 98.7$; $P < 0.0001$.

[f] One-way ANOVA: $F_{(7,48)} = 4.26$; $P = 0.001$. Means followed by different letters are significantly different ($P < 0.05$).

[g] The species *T. radicans*, *S. mombin*, and *S. purpurea* were not included in development time to pupa, pupal wt, or development time to adult analyses as no larvae pupated when fed leaves of these plants.

Table 4. Adult oviposition no-choice tests of *T. elegans*

Plant species	Number of replications	Number of eggs on leaves
S. terebinthifolius	13	75.2 ± 74.3[a]
P. integerrima	5	25.8 ± 32.1[a]
P. vera	5	0.2 ± 0.5[b]

Means followed by a different letter are significantly different (Kruskal-Wallis test and multiple comparisons $P < 0.05$).

in Argentina and Brazil (D'Araujo et al. 1968, Mc Kay et al. 2009, G.S.W. and F.M., unpublished results) suggested a narrow host range. In addition, no *Tecmessa* spp. have been reported as pests in *Pistacia* plantations in Argentina (1,000 ha) (Margheritis and Rizzo 1965, Rizzo 1977, Justo and Parra 2005, Diario de Cuyo 2005), suggesting no threats to cultivated *Pistacia* in the United States. In addition, climatic requirements for *Pistacia* plantations (hot, dry summers, and cool winters) (Servicio Meteorológico Nacional 2000) do not match those suitable for *S. terebinthifolius* and *T. elegans* (tropical conditions with high humidity) (Servicio Meteorológico Nacional 2000). This is supported by the results of the multiple-choice oviposition test (walk-in cage) where *T. elegans* showed a clear preference for its natural host (Table 5). However, the physiological ability of *T. elegans* to complete larval development on *Pistacia* and several other Anacardiaceae species (Tables 2 and 3), and the lack of clear oviposition preference under a no-choice situation (Table 4), make *T. elegans* difficult to recommend as a safe biological control agent.

Details of the biology and life history of *T. elegans* indicate the presence of an exocrine gland on the ventral portion of the first prothoracic segment. In the case of *T. elegans*, the emission of formic acid in response to disturbance might constitute a repellent defense against larval natural enemies as demonstrated in other Notodontidae species (Eisner et al. 1972). Analysis of these gland secretions by GC/MS did not detect additional lipophilic components (G.S.W., unpublished data) as shown in other species of Notodontidae (Eisner et al. 1972, Weatherson et al. 1986, Attygalle et al. 1993).

Both ecologists and biological control practitioners have generalized about the co-evolutionary relationship between plant phylogeny and host range of potential agents (e.g., Berenbaum 1983, Briese 2005). A modern classification of the Anacardiaceae recognizes two infrafamilial groups: subfamily Anacardioideae, including the Anacardieae, Dobineae, Rhoeae, and Semecarpeae tribes and subfamily Spondioideae, including the Spondiadeae tribe (Pell 2004, Mitchell et al. 2006, APG III 2009). We tested members of three of these five tribes; the Anacardieae (*Anacardium* and *Mangifera*), Rhoeae (*Astronium*, *Comocladia*, *Cotinus*, *Lithrea*, *Malosma*, *Metopium*, *Pistacia*, *Rhus*, *Schinopsis*, *Schinus*, and *Toxicodendron*) and Spondiadeae (*Spondias*). Our results suggest that *T. elegans* is primarily restricted to members of the Rhoeae tribe and at least one member of the Anacardieae tribe (e.g., *Anacardium*); but no development was observed on other Anacardieae tribe members *Mangifera* and *Spondias* spp. More members of these subfamilies need to be tested to thoroughly examine the relationship between the phylogeny of the Anacardiaceae and host range of the associated specialized herbivores. Moreover, comparative phytochemical studies need to be conducted to examine biochemical cues that might be used in host plant discrimination in *T. elegans* and other herbivore species.

In conclusion, the results presented here indicate *T. elegans* has a broad fundamental host range, including many ecologically and economically important North American, Hawaiian, and Caribbean plant species. Therefore, we do not recommend this species for the biological control of *S. terebinthifolius* in these infested regions.

Table 5. Adult oviposition in multiple-choice test on *T. elegans* in walk-in cage

Replicates	Total no. of eggs			
	Cage (walls)	*S. terebinthifolius*	*P. vera*	*P. integerrima*
1	225	0	0	0
2	75	60	0	0
3	200	125	0	0
Mean ± SD	166.7 ± 80.4	61.7 ± 62.6	0	0

No statistical analyses were conducted on these data.

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