Damage to *Miconia calvescens* and Seasonal Abundance of *Salbia lotanalis* (Lepidoptera: Crambidae) in Costa Rica

FRANCISCO R. BADENES-PEREZ,[1,2,3] ALEXANDER CASTILLO,[4] AND M. TRACY JOHNSON[5]

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ABSTRACT *Miconia calvescens* de Candolle (Melastomataceae) is an invasive tree considered the most serious threat to natural ecosystems of Hawaii and other Pacific islands. The success of *M. calvescens* as an invasive species is greatly owing to its shade tolerance and the shaded habitat it creates, where many native plant species that are light-demanding cannot survive. *Salbia lotanalis* Druce (Lepidoptera: Crambidae), a neotropical leaf roller attacking *M. calvescens*, was evaluated for two mechanisms by which it reduces leaf area of its host plant: feeding (defoliation), which removes leaf tissue, and tying leaf rolls, which reduces exposed area of leaves. These impacts were quantified over a 1-yr period at a field site in Costa Rica, where densities of *S. lotanalis* larvae attacking *M. calvescens* peaked at the end of the rainy season and declined in the dry season. Up to 47.5% of leaves were attacked by *S. lotanalis*, with cumulative defoliation by an undetermined number of larvae removing an average of ≈30% (253 cm^2) of each leaf attacked. Defoliation and leaf rolling were compared in a greenhouse experiment in which individual *S. lotanalis* larvae defoliated an average of 3.7% (17.8 cm^2) of each attacked leaf, and reduced exposed leaf area as a result of leaf rolling by an average of 12.8% (66.2 cm^2). Our results complement the findings of previous studies of *S. lotanalis* and confirm its potential as a biological control agent of *M. calvescens*.

KEY WORDS leaf roller, defoliation, leaf area

The velvet tree, *Miconia calvescens* de Candolle (Myrtales: Melastomataceae), is a small tree native to Central and South America that is present as an invasive species in Hawaii and other Pacific islands, where it is considered a serious threat to native ecosystems (Denslow et al. 1990, Meyer and Florence 1996, Medeiros et al. 1997). Success of *M. calvescens* as an invasive species is partly owing to its shade tolerance, which allows it to thrive in understory habitats, including the dense shade cast by mature *M. calvescens* that excludes smaller light-demanding native plants (Meyer and Florence 1996, Medeiros et al. 1997).

Classical biological control with natural enemies from its native range is considered an essential tool for long-term management of *M. calvescens* (Smith 2000, Kaiser 2006, Johnson 2010). A variety of neotropical arthropods and pathogens have been evaluated as potential biological control agents of *M. calvescens* in recent years, but so far only a fungal pathogen has been released in Hawaii and Tahiti (Killgore 2002, Barreto et al. 2005, Picanço et al. 2005, Badenes-Perez et al. 2008, Hanson et al. 2010, Conant et al. 2013). Among insects evaluated as potential agents, *Salbia lotanalis* Druce (Lepidoptera: Crambidae), whose larvae tie leaves producing large leaf rolls within which they feed, has been the subject of biology and host-specificity studies in Brazil (Morais et al. 2010, 2012) and Costa Rica (Castillo 2009, Castillo et al. 2014). The insect has five larval instars and completes one generation in 60–90 d (Morais et al. 2010, Castillo et al. 2014). Host-specificity testing in Brazil showed that third-instar *S. lotanalis* feed and develop successfully on *M. calvescens* and *Clidemia hirta* (L.) D. Don (Melastomataceae), but not on other Melastomataceae (Morais et al. 2012). In greenhouse experiments conducted in Brazil, defoliation by *S. lotanalis* larvae reduced leaf area, leaf number, and plant height in 1-yr-old *M. calvescens* plants (Morais et al. 2010).

In Hawaii and other locations where *M. calvescens* is invasive, *S. lotanalis* could impact *M. calvescens* trees in two ways: through defoliation as a result of larval feeding and through leaf rolls that decrease the leaf area exposed to sun. Defoliation and leaf rolling could reduce photosynthesis and plant fitness, and also reduce shading by *M. calvescens* trees, improving survival of native plants beneath. The objectives of this study were to quantify and compare these two different impacts of herbivory and to explore the effect of seasonal abundance of *S. lotanalis* on *M. calvescens* in Costa Rica.

[1] Pacific Cooperative Studies Unit, University of Hawaii at Manoa, Honolulu, HI 96822.

[2] Current address: Instituto de Ciencias Agrarias, CSIC, 28006 Madrid, Spain.

[3] Corresponding author, e-mail: frbadenes@ica.csic.es.

[4] Escuela de Biología, Universidad de Costa Rica, San Pedro de Montes de Oca, San José, Costa Rica.

[5] Institute of Pacific Islands Forestry, Pacific Southwest Research Station, USDA Forest Service, Volcano, HI 96785.

Materials and Methods

Description of Test Site. *M. calvescens* is uncommon in its native range, restricted to secondary vegetation, forest edges, and forest gaps (Denslow et al. 1990, Ellison et al. 1993, Meyer 1998). To create dense populations of *M. calvescens* and attract potentially host-specific herbivores, saplings were planted in 2003 at a variety of field sites in central Costa Rica. Survival of plants was poor at most sites, especially those outside the natural distribution of *M. calvescens* (Johnson, unpublished data). One site where *M. calvescens* established well was in Sabanilla de Montes de Oca (09° 56′48″ N, 84° 02′45″ W, 1,200 m above sea level), in highly disturbed suburban San José Province, ≈60 km from the nearest natural populations of *M. calvescens.* This site became particularly interesting for consistently attracting populations of *S. lotanalis*, which was not encountered in other parts of Costa Rica where *M. calvescens* occurs (Badenes-Perez et al. 2010).

The site at Sabanilla de Montes de Oca was planted with 100 young *M. calvescens* in 2003 at a density of roughly 1 tree per square meter. By the time this study begun in November 2006, most trees were ≈2 m in height. The site had an average annual temperature of ≈20°C, 87% relative humidity (RH), and rainfall of 1,800–2,000 mm, with a relatively severe dry season lasting ≈4 mo. Greenhouse studies were conducted 1 km away from the field site at the School of Biology, University of Costa Rica, from October 2006 to February 2007, under natural photoperiod, 20 ± 5°C, and 85 ± 7% RH.

Seasonal Abundance of *S. lotanalis*. Insect densities were assessed at the field site during the last 3 d of each month from November 2006 through October 2007, and at one instance 5 yr later in September 2012. During each sampling, 10 *M. calvescens* trees were selected at random, and from each tree, five leaves with leaf rolls (caused exclusively by *S. lotanalis* at this site) were selected randomly. Numbers of *S. lotanalis* larvae per leaf were counted nondestructively by gently unrolling each leaf roll in the field. Densities of *S. lotanalis* larvae per rolled leaf from November 2006 through October 2007 were compared using one-way analysis of variance. Insect densities were compared against weather data (monthly averages of temperature, relative humidity, and rainfall) using linear regression. Data from a nearby weather station, also in Sabanilla de Montes de Oca, were provided by the Instituto Meteorológico Nacional de Costa Rica (http://www.imn.ac.cr/). Voucher specimens of *S. lotanalis* were deposited in the Zoology Museum of the Department of Biology at the University of Costa Rica.

Defoliation and Leaf Rolling by *S. lotanalis* on *M. calvescens* in the Field. On each of the 10 randomly selected trees, the total number leaves with and without leaf rolling were counted in November 2006, March 2007, and September 2012. November and March were chosen because they correspond to the approximate endpoints of the rainy and dry seasons, respectively, which we previously had observed to markedly affect growth and leaf drop of *M. calvescens* in this habitat (Allen 2010). Plants were resampled 5 yr later in September 2012 to see if *S. lotanalis* continued to impact this site.

In March 2007, after densities of *S. lotanalis* larvae had peaked and declined and damage to leaves was at a potential maximum, defoliation was quantified for 10 leaves randomly selected from those with *S. lotanalis* leaf rolls (1 leaf per tree). The collected leaves were unrolled, pressed flat, and digitally photographed for leaf area analysis using WinFOLIA software (Regent Instruments Inc., Quebec City, QC, Canada). In cases of extensive defoliation, leaf margins (defining leaf area in absence of damage) were approximated manually based on symmetry and comparison with leaves of similar size. Leaf area after feeding by *S. lotanalis* was compared with estimated leaf area in the absence of *S. lotanalis* feeding using a paired *t*-test.

Defoliation and Leaf Rolling by *S. lotanalis* on *M. calvescens* in the Greenhouse. Damage by a single *S. lotanalis* larva was quantified in the greenhouse by placing 40 field-collected first-instar larvae individually on 40 leaves (one larva per leaf) of young potted *M. calvescens* (≈1 m in length). Larvae were distributed over the 10 plants (four larvae per plant). Data were recorded as leaf area defoliated and leaf area affected by leaf rolling after each larva had pupated. Two digital photographs were taken of each leaf, one with the leaf roll intact and another with the leaf unrolled, allowing separate estimations of leaf area reduction owing to leaf rolling and defoliation by *S. lotanalis* larvae. Leaf area in the photographs was measured using WinFOLIA software (Regent Instruments Inc. 2011, Nepean, ON, Canada). The relationship between leaf size (total leaf area estimated in the absence of damage) and leaf area reduction as a result of leaf rolling was evaluated using linear regression. Leaf area after feeding by *S. lotanalis* was compared with estimated leaf area in the absence of *S. lotanalis* feeding using a paired *t*-test.

Results

Seasonal Abundance of *S. lotanalis*. Larvae of *S. lotanalis* were found at every sampling date between November 2006 and October 2007, and even 5 yr later in September 2012. Densities of *S. lotanalis* larvae per rolled leaf varied significantly over 2006–2007 (Fig. 1; $F = 3036.59$; df = 11, 137; $P \leq 0.0001$), peaking at the end of the rainy season (November) and declining to a low point at the end of the dry season (April–May). Densities of *S. lotanalis* larvae had a significant positive correlation with certain climatic parameters (Table 1), particularly relative humidity in the preceding 1–3 mo and rainfall in the preceding 1–2 mo. Relative humidity and rainfall were positively correlated ($R^2 = 0.66$; $y = 83.45 + 0.021x$; $n = 12$; $P = 0.001$). Densities of *S. lotanalis* larvae showed a significant negative correlation with average and maximum temperatures.

Based on the number of larvae per leaf in the leaves sampled (Fig. 1) and the number of leaves with leaf rolling per tree (Table 2), the densities of *S. lotanalis*

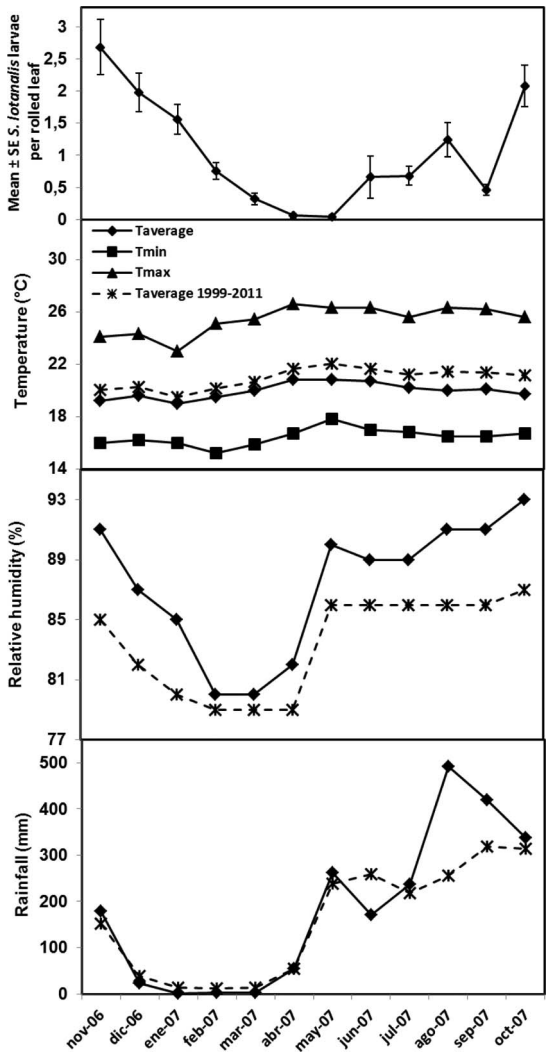

Fig. 1. Seasonal abundance of *S. lotanalis* on *M. calvescens* as mean number of larvae (±SE) per rolled leaf, and monthly means for temperature, relative humidity, and rainfall in Sabanilla de Montes de Oca, San José, Costa Rica, between November 2006 and October 2007. A dashed line is used to show averages of monthly means for temperature, relative humidity, and rainfall for 1999–2011 (data provided by the Instituto Meteorológico Nacional de Costa Rica).

larvae per tree were estimated at 107.2 ± 6.7, 5.3 ± 1.9, and 89.7 ± 11.8 (mean ± SE) for November 2006, March 2007, and September 2012, respectively. Larvae within a single leaf roll were often different instars, indicating reuse of existing rolls by successive cohorts. Besides *S. lotanalis* larvae, other arthropods found in leaf rolls included earwigs, spiders, and adult chrysomelid beetles.

Defoliation and Leaf Rolling by *S. lotanalis* on *M. calvescens* in the Field. Incidence of leaf rolling by *S. lotanalis* averaged between 33.2 and 47.5% of leaves per tree (Table 2), with no statistically significant differences across three sample dates ($F = 3.11$; df = 2, 27; $P = 0.061$). Leaf rolls were found in young to fully expanded leaves. Two to three leaves as small as 5-cm in length, near the apical bud, were sometimes found tied together with the silk threads secreted by individual *S. lotanalis* larvae. Although most often only one roll was found per leaf, in large leaves we sometimes found several leaf rolls (up to 4), the largest measuring 45 cm in length. There was a significant 51% reduction in number of leaves per tree from November 2006 to March 2007 (Table 2; $t = 7.01$; df = 9; $P < 0.001$). The number of leaves per tree was significantly higher in September 2012 compared with the previous sampling dates, as trees were 5 yr older and sampling took place during the period of vegetative growth before onset of the dry season.

In March 2007, after *S. lotanalis* larvae had fed for several months and then declined in number, *M. calvescens* leaves affected by leaf rollers had an average defoliation of 252.8 ± 43.7 cm^2 per leaf (29.8 ± 3.4%; mean ± SE). Sampled leaves had an average leaf area of 836.6 ± 80.2 cm^2, estimated in the absence of *S. lotanalis* damage. Leaf rolls in these leaves usually showed necrotic windowing and foliage browning, indicating that the damage by *S. lotanalis* was not recent.

Defoliation and Leaf Rolling by *S. lotanalis* on *M. calvescens* in the Greenhouse. Individual *S. lotanalis* larvae developing from first instar to pupation on one *M. calvescens* leaf consumed an average of 17.8 ± 1.9 cm^2 (3.7 ± 0.4% of the leaf, mean ± SE). As a result of leaf rolling, these larvae reduced exposed leaf area by an average of 66.2 ± 8.4 cm^2 (12.8 ± 1.4% of the unrolled leaf, mean ± SE). Leaves where *S. lotanalis* fed on potted greenhouse plants had an average leaf area of 546 ± 41 cm^2 (mean ± SE). Larger leaves supported larger leaf rolls, as indicated by a significant positive relationship between leaf size (total leaf area) and leaf area reduction (in cm^2) as a result of leaf rolling ($y = 2.9 + 0.1x$; $n = 40$; $R^2 = 0.32$; $F = 18.08$; $P \leq 0.001$).

Discussion

The impact of defoliation of *M. calvescens* by *S. lotanalis* larvae is compounded by leaf area reduction as a result leaf rolling. As a potential biological control agent, *S. lotanalis* could decrease *M. calvescens* fitness and reduce the dense shading that contributes to the devastating impact of *M. calvescens* on native understory vegetation in invaded Pacific Islands (Meyer and Florence 1996, Medeiros et al. 1997). In Tahiti, partial defoliation (5–35%) of *M. calvescens* trees by the fungal pathogen *Colletotrichum gloeosporioides* f. sp. *miconiae* increased the abundance and growth of several native plants, especially light-demanding species (Meyer and Fourdrigniez 2011, Meyer et al. 2012). At our field site, we observed ≈50% of leaves with *S. lotanalis* leaf rolls, sometimes more than one per leaf, indicating the potential of significant impact from leaf rolling alone. Our greenhouse experiment showed that, through leaf rolling only, one *S. lotanalis* larva can reduce exposed leaf area by an average of 12.8%, an

Table 1. Linear regressions between density of *S. lotanalis* (mean larvae per rolled leaf) and monthly climate data ($n = 12$)

Climatic parameter[a]	Regression formula	R^2	F	P
Relative humidity (same month)	$y = -5.8 + 0.1x$	0.17	2.03	0.184
Relative humidity (1 mo before)	$y = -11.1 + 0.1x$	0.54	11.54	0.007*
Relative humidity (2 mo before)	$y = -12.0 + 0.1x$	0.62	16.26	0.002*
Relative humidity (3 mo before)	$y = -9.5 + 0.1x$	0.40	6.74	0.027*
Relative humidity (4 mo before)	$y = -3.2 + 0.05x$	0.07	0.71	0.419
Rainfall (same month)	$y = 1.0 + 0.0001x$	0.01	0.01	0.929
Rainfall (1 mo before)	$y = 0.7 + 0.002x$	0.19	2.31	0.159
Rainfall (2 mo before)	$y = 0.3 + 0.004x$	0.71	24.65	<0.001*
Rainfall (3 mo before)	$y = 0.2 + 0.005x$	0.83	47.88	<0.001*
Rainfall (4 mo before)	$y = 0.6 + 0.003x$	0.27	3.75	0.082
Avg temp (same month)	$y = 23.1 - 1.1x$	0.59	14.50	0.003*
Avg temp (1 mo before)	$y = 11.3 - 0.51x$	0.13	1.46	0.255
Avg temp (2 mo before)	$y = -0.1 + 0.06x$	0.00	0.01	0.904
Max temp (same month)	$y = 14.2 - 0.52x$	0.44	7.80	0.019*
Max temp (1 mo before)	$y = 5.0 - 0.16x$	0.04	0.42	0.304
Max temp (2 mo before)	$y = -5.4 + 0.25x$	0.11	1.17	0.408
Min. temp (same month)	$y = 8.5 - 0.46x$	0.12	1.37	0.269
Min. temp (1 mo before)	$y = -0.9 + 0.12x$	0.01	0.08	0.782
Min. temp (2 mo before)	$y = -4.6 + 0.35x$	0.07	0.75	0.408

[a] The units of the climatic parameters were percent (for relative humidity), mm (for rain), and degrees Celsius (for temperature).
* Linear correlation statistically significant at $P \leq 0.05$.

impact greater than larval feeding, which removed 3.7% of the same leaves on average.

Defoliation by *S. lotanalis* appeared to accumulate over sampling dates, with successive cohorts attacking the same leaves. Cumulative damage by undetermined numbers of *S. lotanalis* larvae per leaf resulted in substantial defoliation: 23.3% of the leaf area of attacked leaves. By the end of the dry season in March 2007, trees had lost half their leaves compared with the previous November. Feeding by *S. lotanalis* larvae can make *M. calvescens* leaves fall off (Castillo 2009, Morais et al. 2010, Castillo et al. 2014); however, some loss of foliage is typical for *M. calvescens* during the relatively severe dry season in San José Province (Johnson, unpublished data). Thus, seasonal drought probably explains the decline of *S. lotanalis* densities observed in this study. The correlation between *S. lotanalis* densities and rainfall in previous months suggests that rainfall might have affected *S. lotanalis* indirectly via the status of the plant. It is unknown if *S. lotanalis* can undergo quiescence as a result of dry conditions, but this type of quiescence could also be responsible for the decline in larval densities we observed. Climate at the field site during our year of observations was typical of the long-term average in Sabanilla de Montes de Oca (Fig. 1; http://www.imn.ac.cr). The consistent presence of abundant *S. lotanalis* leaf rolls at this site over our sampling dates, including 5 yr after our initial study, suggests that this is a stable, reliable herbivore–plant interaction.

While dry conditions appear to be a limiting factor for *S. lotanalis* development at the Costa Rica site, climatic conditions may be more favorable for *S. lotanalis* in Hawaii. In the areas most infested by *M. calvescens* in Hawaii (Hilo and Hana), temperatures are mild (20–27°C) and rainfall is relatively constant and abundant (200–300 mm per month, >2,000 mm year), without a marked dry season (www.wrcc.dri.edu/; Juvic and Juvic 1998). Another neotropical leaf rolling *Salbia* species, *Salbia haemorrhoidalis* Guenée, released for biological control of *Lantana camara* L. (Verbenaceae) in South Africa, developed higher densities in moist areas than in dry areas (Baars 2003).

S. lotanalis are easy to rear in the laboratory, have a short life cycle and a high reproductive rate, and appear to be restricted to *M. calvescens* and other Melastomataceae (Castillo 2009, Janzen and Hallwachs 2009, Morais et al. 2012, Castillo et al. 2014), traits that appear to make it a suitable candidate for biological control. Feeding by *S. lotanalis* larvae has been shown to reduce growth of *M. calvescens* in greenhouse conditions (Morais et al. 2010), and our results suggest that defoliation and leaf rolling by *S. lotanalis* larvae could substantially reduce leaf area and shade produced by *M. calvescens.* However, efficacy of *S. lotanalis* against *M. calvescens* outside its native range will also depend on biotic factors affecting population growth. At our study site in Costa Rica, *S. lotanalis* larvae and pupae were rarely parasitized (Castillo 2009, Castillo et al. 2014), and in Brazil parasitism was

Table 2. Number of leaves and frequency of leaf rolling (mean ± SE) per tree on three sampling dates

Sampling date	Total leaves per tree	Leaves with leaf rolling (%)	Leaves with 1 leaf roll (%)	Leaves with 2 leaf rolls (%)	Leaves with ≥3 leaf rolls (%)	Leaf rolls per leaf in leaves with leaf rolling
Nov. 2006	83.4 ± 5.7	47.5 ± 4.3	32.7 ± 2.6	12.7 ± 1.5	2.1 ± 0.5	1.4 ± 0.0
Mar. 2007	40.5 ± 3.9	44.0 ± 4.1	37.4 ± 3.5	6.6 ± 1.3	0.0 ± 0.0	1.2 ± 0.0
Sept. 2012	142.2 ± 15.8	33.2 ± 4.9	23.5 ± 3.5	9.2 ± 1.9	0.6 ± 0.2	1.3 ± 0.0

<10% as well (Morais et al. 2012). Unfortunately, high levels of parasitism seem likelier in Hawaii, where the congeneric *S. haemorrhoidalis* introduced to control *L. camara* is apparently substantially suppressed by parasitism or climate (Broughton 2000). However, populations of *S. haemorrhoidalis* in some areas of South Africa caused significant impact on *L. camara* despite relatively high parasitoid pressure (Baars 2003). Further assessment of the potential impacts of natural enemies on *S. lotanalis* is needed. Although prospects for biotic interference in Hawaii appear high, this might not be the case in Tahiti and other areas where *M. calvescens* is invasive (Meyer and Florence 1996, Murphy et al. 2008).

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