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Biology of the leaf roller *Salbia lotanalis* and its impact on the invasive tree *Miconia calvescens*

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Abstract *Miconia calvescens* (Melastomataceae) is an invasive alien tree in native forests on some Pacific islands and a potentially invasive species in Australia. Searches for potential classical biocontrol agents have been undertaken for over a decade in the centre of origin (Central and South America). *Salbia lotanalis* (Lepidoptera: Pyralidae) is a leaf roller which has been recognized as a promising classical biocontrol agent for *M. calvescens*. This paper presents the biology and an impact study of *S. lotanalis* on *M. calvescens.* Life table parameters showed that *S. lotanalis* has a high reproductive capacity, with up to six generations a year. *Miconia calvescens* seedlings attacked by *S. lotanalis* caterpillars had their growth rate significantly reduced. Seedlings subjected initially to a high level of defoliation (80%) caused by caterpillars had leaf fall and a lower leaf area than controls after 210 days. Considering the high population growth rate and significant impact on young plants, *S. lotanalis* appears to have a high potential for use as a classical biological control agent to be used against *M. calvescens*.

Keywords Classical biocontrol · Melastomataceae · Lepidoptera: Pyralidae · Fertility life table · Defoliation · Pacific islands

Introduction

Miconia calvescens DC. (Melastomataceae) is a small tree native to Central and South America that has invaded forest ecosystems in French Polynesia, Hawaii, New Caledonia and Australia, where it was introduced as an ornamental (Csurhes 1997; Medeiros et al. 1997; Meyer 1996). *Miconia calvescens* is among the one hundred worst weeds of the world (Lowe et al. 2000), and in Australia it has been declared a class one weed (the highest priority category) (Murphy et al. 2008). Success of *M. calvescens* invasion in these places is due its high reproductive capacity and adaptation to rain forest environments. *Miconia calvescens* impacts include competition with native plants, alteration of forest community composition, and its threat to endangered plant, bird and invertebrate

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species (Medeiros et al. 1997; Meyer and Florence 1996).

Miconia calvescens has been a target for biological control for over a decade and searches for natural enemies have yielded numerous pathogens (Seixas et al. 2004; Seixas et al. 2007; Seixas et al. 2002) and phytophagous arthropods (Badenes-Perez and Johnson 2007a, b, 2008; Burckhardt et al. 2005; Burckhardt et al. 2006; Picanço et al. 2005). Of these potential agents, only an anthracnose causing fungus (*Colletotrichum gloeosporioides* f.sp. *miconiae* Killgore, Sugiyama and Barreto) was introduced into Hawaii and French Polynesia from Brazil (Seixas et al. 2007). It has established both in Hawaii and in French Polynesia, and while impact has been significant in the latter, introduction of additional agents is required to increase the control efficiency (Meyer et al. 2008).

Preliminary surveys for arthropods attacking *M. calvescens* in Brazil indicated that *Salbia lotanalis* Druce (Lepidoptera: Pyralidae) is a promising biocontrol agent to be used against this weed (Picanço et al. 2005). Initially, this lepidopteran was wrongly identified as *Ategumia* sp. (Lepidoptera: Pyralidae), and later its identity was clarified as *S. lotanalis* by Dr. Vitor Osmar Becker (University of Brasilia, Brazil). *Salbia lotanalis* is a defoliator. Their caterpillars roll leaves longitudinally, forming tubes within which they feed and eventually pupate (Picanço et al. 2005). In the field, mature and juvenile plants of *M. calvescens* were commonly found with a high level of defoliation by this leaf roller, and some plants were dead, seemingly after severe attacks by *S. lotanalis* (Morais unpublished observations).

Many Lepidoptera species have been used in biological control of weeds (Baars 2003; Ostermeyer and Grace 2007), while others have been considered as potential agents (Dhileepan et al. 2007; Williams and Madire 2008), including for *M. calvescens* (Badenes-Perez and Johnson 2008; Picanço et al. 2005). A closely related leaf roller, *Salbia haemorrhoidalis* Gueneé (Pyralidae), is regarded as highly successful biocontrol agent for the weed *Lantana camara* L. (Verbenaceae) in South Africa (Baars 2003).

Classical biological control of weeds by phytophagous insects and plant pathogens is an appropriate management technique for this invader, insofar as control efforts by chemical (herbicides) and mechanical (removal) means are expensive and inefficient (Kaiser 2006; Smith 2002). Before recognition of any natural enemy of a weed as a good biocontrol candidate in a classical biocontrol program, several studies are necessary, including those leading to precisely identifying the organism, development of methods of raising it under controlled conditions, host-range evaluation, elucidation of life-cycle and evaluating its natural enemies and potential impact on the host plant, among others (Julien 1997). Ecological approaches also contribute to selection of biocontrol agents and pre-release evaluation of the potential impact of herbivory on plants, for example, may increase the success in biological control and reduce ecological risk (Goolsby et al. 2004; Louda et al. 2003).

The life history of a potential biological control agent can be used to predict its performance in the introduction area (Harley and Forno 1992). Life tables are good tools for evaluating population dynamics of the biocontrol agent, inasmuch as they provide data on the development, mortality and survival rates, and reproductive capacity of the population (Price 1997).

Impact studies can help identify biocontrol agents of a weed with the highest impacts on plant productivity and growth rates, narrowing the prospective list of biological control agents and helping prioritize agents for management. Analyses of successful biological control programs have shown that in 50% of the cases with introduction of multiple agents, a single agent was responsible for effecting control (Denoth et al. 2002), because some agents appear to be ineffective or interactions among agents are antagonistic (Raghu and Dhileepan 2005). Further, plants can vary in their response to damage, increasing growth or showing a compensatory effect after herbivory (Strauss and Agrawal 1999). Therefore, experiments for determining the effects of herbivory on weeds are essential in the selection of effective biocontrol agents. In this paper we provide information on rearing methodology, the biology through life tables and an impact study of *S. lotanalis* on *M. calvescens.*

Materials and methods

Life cycle experiment

Life cycle and life table experiments were carried out at the Integrated Pest Management Laboratory, Department of Animal Biology, Federal University

of Viçosa, Brazil, and were conducted in a rearing room with a light regime of 12:12 and with ambient air temperature and relative humidity which were monitored daily during all experiments.

Caterpillars of *S. lotanalis* that were attacking *M. calvescens* in the field were collected and brought to the laboratory. The caterpillars were put in 40 × 50 cm plastic bags with leaves of *M. calvescens* inside. These bags were maintained in a rearing room until the caterpillars turned into pupae. Pupae were separated by sex and placed into plastic pots with wet vermiculite to avoid desiccation. The determination of sexes was done according the characters described by Butt and Cantu (1962). Differences of sex in pupae of *S. lotanalis* could be easily visualized, since females have a suture on genital plate that extends to the seventh abdominal segment, while the male suture is only on eighth abdominal segment (arrows on Fig. 1F, G indicates these sutures).

When the adults emerged they were transferred to cages (0.5 × 1.0 × 1.0 m) enclosed in organza, with a young *M. calvescens* plant (0.8–1.0 m high) inside. Four cages were used and ten breeding pairs of *S. lotanalis* were placed in each cage. The adults were fed with a 10% honey solution.

After the eggs from these adults hatched, 30 caterpillars were transferred individually to a *M. calvescens* leaf. Leaves were placed in numbered 40 × 50 cm plastic bags. Head capsule width, length and corporal width of the caterpillars were assessed every two days. Caterpillars were weighed on an analytical balance with a precision of 10^{-2} mg. Measurements were done with a Leica MZ75 stereoscopic microscope attached to a digital camera, where the caterpillars were also photographed. Photographs were processed in the Leica Qwin program, with which biometric data was also obtained. Twenty individuals of each stage (egg, larva, pupae and adult females and males) were measured, and their colors and behavior were recorded. The number of instars for *S. lotanalis* was determined using the Brooks-Dyar rule that involves analyzing the frequency distribution of head capsule widths and the progression of larval growth (Daly 1985).

Lifespan and fertility life tables

Life table data were obtained during two life cycles: the first from May 09, 2005 to July 19, 2005 and the second from June 22, 2006 to October 01, 2006. Ten pairs of adults were transferred to the same four cages used in the life cycle study with *M. calvescens* seedlings. The adults were also fed with a 10% honey solution. After eggs hatched, thirty caterpillars were transferred individually to *M. calvescens* leaves into numbered plastic bags maintained in a rearing room. The instar of the caterpillar and their survival were recorded daily. When the caterpillars transformed into a pupa, they were separated by sex into plastic pots with wet vermiculite. After all adults emerged, the number of dead pupae were counted. Adults were transferred to a cage with a *M. calvescens* seedlings. Daily, egg numbers, females and males were counted until all adults died.

Life expectancy and fertility tables were constructed from the survival and oviposition data, according to the methods described by Price (1997) and Southwood and Henderson (2000). A survival graph and the accumulated number of females as a function of time were drawn from data in the tables.

Impact study

An impact study was carried out by submitting young *M. calvescens* plants to two defoliation levels: 30% and 80%. The control consisted of plants which were not defoliated. A defoliation level of 100% was not used because *M. calvescens* usually died when completely defoliated by *S. lotanalis* caterpillars (Morais unpublished observations). Young plants used in this experiment were one year old, had 8–10 leaves and were 0.80–1.00 m tall. Seeds were extracted from fresh ripe fruits on *M. calvescens* trees which were in the field and germinated in a box with sand. After three months, when seedlings were approximately 10 cm tall, they were transplanted to 5 l pots with soil. Before transplanting, each pot received 50 g of 4–14–8 mineral fertilizer (N–P-K) and these seedlings were irrigated daily.

The level of defoliation required was obtained by protecting some leaves with organza bags. For example, if the plant had ten leaves, in order to obtain 30% or 80% defoliation, seven or two leaves were protected with organza bags, respectively. Defoliation was produced by two *S. lotanalis* caterpillars of the 4th and 5th instar placed on each leaf. Caterpillars stayed on the plant for two weeks until all unprotected leaves became defoliated. Controls

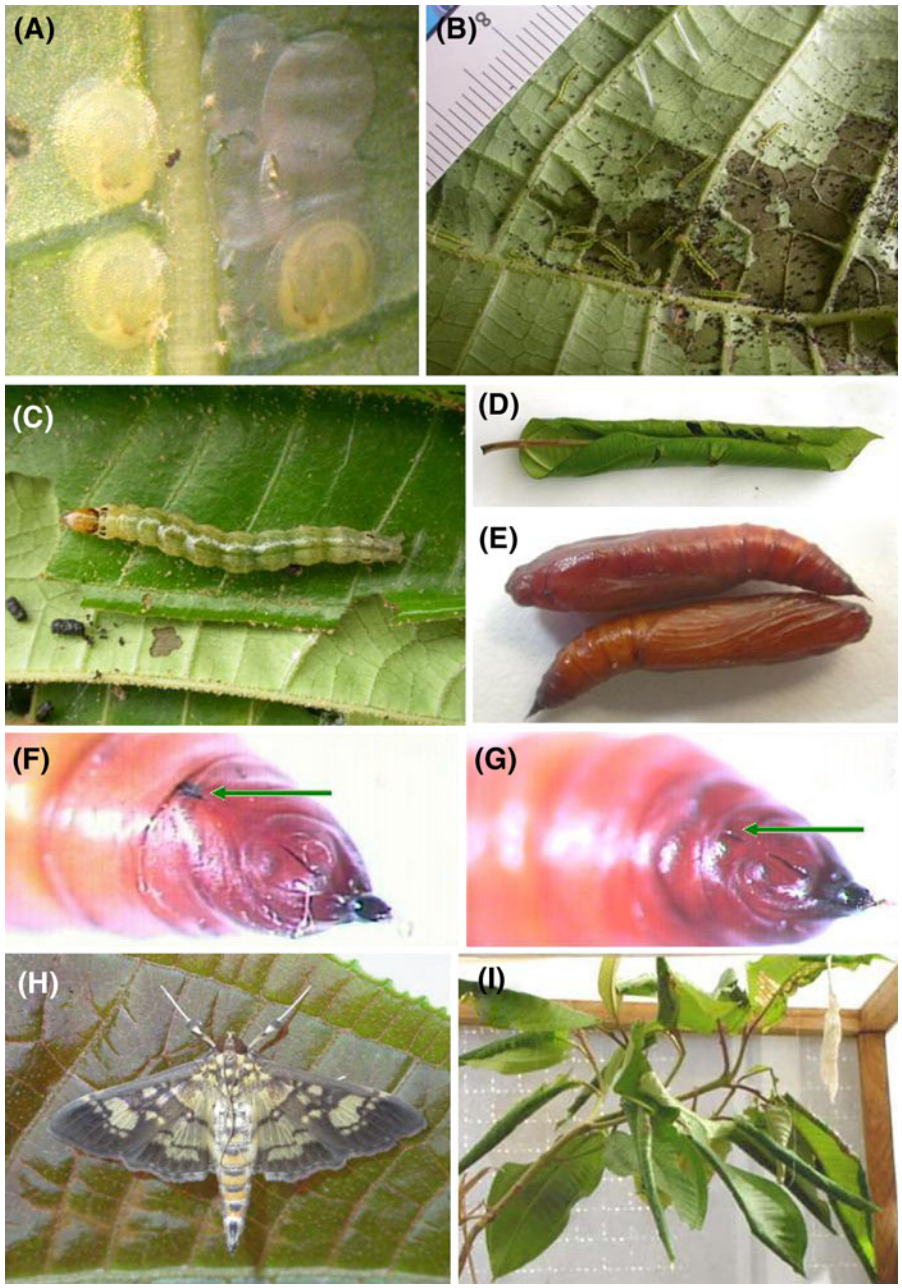

Fig. 1 *Salbia lotanalis*: eggs (**A**), first instar caterpillar (**B**), fifth instar caterpillar (**C**), pupa (**E**), female pupa (**F**), male pupae (**G**) and adult (**H**); *Miconia calvescens:* leaf (**D**) and seedling (**I**) attacked by *Salbia lotanalis*. Green arrows on pupae indicate the sutures used to separate the sexes

were maintained in the same conditions but did not receive any caterpillars.

After defoliation, the seedlings were transplanted to an area at the Botanic Garden of the Universidade Federal de Viçosa, Brazil. This area is at the margin of a secondary forest where vegetation is composed of small shrubs and grasses. All plants within a one meter circle around the newly planted *M. calvescens* plants were removed in order to avoid competition and allow an easy evaluation of plant development. A randomized block experimental design with four replicates and three treatments (levels of defoliation)

was used. Each block was composed of two *M. calvescens* seedlings of each treatment, arranged in rows with 2.0 m space between rows and 1.5 m between plants within a row. Beginning two weeks after the seedlings were transplanted, the following features were assessed at two-week intervals until 216 days after defoliation (approximately seven months): number of leaves and nodes, plant height and distance between nodes.

Leaf area was determined by photographing all leaves on seedlings under a drawing board with a ruler. Pictures were analyzed in the QuantPoro v.1.0.2 program, where leaf area was calculated. The QuantPoro program was developed in the Department of Soil of the Federal University of Viçosa. This program processes and analyzes images and measures or evaluates the morphological characteristics of objects and has often been used in micromorphometric analysis of soil aggregates.

Data analysis of impact study

Plant characteristics were individually subjected to repeated-measures ANOVA, with time (days after the defoliation) as the within subjects factor. Significant differences between treatments were identified using Bonferroni *t*-tests as the *post hoc* procedures, at a significance level of $P < 0.05$. Statistical analyses were performed using the SAS procedure ANOVA with the REPEATED/PROFILE statement. Only curves of plant characteristics assessed with significantly different treatment were represented in function of the defoliation.

Results

Life cycle

Salbia lotanalis eggs are round and yellow. They are laid individually or in groups of three to six on the abaxial leaf surface. Before the eggs hatch, they become transparent, and it is possible to see the caterpillar inside (Fig. 1A).

A multimodal curve of frequency of head capsule width had five peaks, showed that *S. lotanalis* has five larval instars ($F = 625.99$; d.f. = 24, 29; $P = 0.0016$). As head capsule width increased, so did the probability of misclassification. Average and amplitude of head capsule width (mm) in first instar was 0.37 (0.24–0.50), in second instar 0.61 (0.56–0.73), in third instar 0.91 (0.75–1.15), in fourth instar 1.32 (1.19–1.50) and in fifth instar 1.66 (1.55–1.75). Growth ratio was 1.43 ($\ln Y = -1.14 + 0.36X$; $R^2 = 99.68$).

Caterpillars of the first instar are green, with a transparent head capsule and black eyes (Fig. 1B). Caterpillars of the second instar are a darker green than first instar, with four black patterns on the body, two on the second and eighth abdominal segments each. Caterpillars of the first and second instar stay on the abaxial leaf surface, where they feed, construct a web over themselves and adhere their excretions.

Caterpillars of the third, fourth and fifth instars are green with six black patterns on the body (four on second abdominal segment and two on the eighth) (Fig. 1C). After the third instar, caterpillars roll the leaf and construct a cylinder that they live inside (Fig. 1D, I). Caterpillars were pink, passing to yellow coloration before transforming into pupa.

Salbia lotanalis pupae are brown and two days before adult emergence it is possible to see the wings inside (Fig. 1E). Female pupae have a suture on the genital plate that extends to the seventh abdominal segment, while male pupae have the suture only on the eighth abdominal segment (Fig. 1F, G). Adults are little brown moths with yellowish patterns on the wing and on the abdomen. Average wing-span is 17 mm and adult length is 14.5 mm (Fig. 1H). Morphometric measurements and the time that *S. lotanalis* remained in each phase (duration) in both sampling periods are presented in Table 1.

Life tables

The duration of *S. lotanalis* and its generation time (T) were longer in the second life cycle (89.65 days) than in the first (61.02 days). Therefore, the time necessary for the population to double in number (DT) starting from adults was also shorter in the first life cycle (14.72 days) than the second life cycle (27.11 days).

Females of *S. lotanalis* began to lay eggs at 58 days of age in the first life cycle and 88 days in the second life cycle. The net reproductive rate (R_0) and gross reproductive rate (GRR) were larger in the first life cycle (17.07 and 28.39 females/female, respectively) than in the second life cycle (9.90, and 18.65 females/female, respectively). The intrinsic

Table 1 Mean ± standard error of morphometric data of 20 individuals and the duration of stages in the life cycle of *Salbia lotanalis*

Stages	Dimensions of the stage		Duration (days)	
	Length (mm)	Width (mm)	First life cycle	Second life cycle
Egg	1.15 ± 0.02	0.86 ± 0.02	10.05 ± 0.05	10.20 ± 0.14
1st instar	3.71 ± 0.11	0.44 ± 0.01	3.05 ± 0.05	6.10 ± 0.10
2nd instar	7.32 ± 0.18	0.85 ± 0.02	4.57 ± 0.25	9.86 ± 0.27
3rd instar	11.41 ± 0.36	1.30 ± 0.03	5.81 ± 0.35	12.57 ± 0.54
4th instar	17.79 ± 0.40	2.10 ± 0.05	8.30 ± 0.60	13.05 ± 0.47
5th instar	23.10 ± 0.47	2.91 ± 0.04	11.53 ± 0.40	14.40 ± 0.57
Pupa (female)	13.07 ± 0.34	3.02 ± 0.07	14.60 ± 0.40	19.32 ± 0.85
Pupa (male)	12.37 ± 0.40	2.89 ± 0.07	14.00 ± 0.39	18.43 ± 0.68
Adult (female)	14.58 ± 1.84	2.93 ± 0.37	13.31 ± 0.58	12.10 ± 0.34
Adult (male)	14.63 ± 2.63	2.98 ± 0.20	14.38 ± 0.65	12.94 ± 0.81

rate of increase (r_m) and the finite rate of increase (λ) were 0.05 and 1.05 in the first life cycle and 0.03 and 1.03 in the second, respectively. These values of $\lambda > 1$ indicate the population was increasing. The maximum reproductive value (V_x) of *S. lotanalis* was also registered in the first life cycle (26.31) at the 58 day of life.

The intersection of the specific fertility curve (m_x) with the survival rate (l_x) was after the 58th day of age in the first life cycle and after the 88th in the second (Fig. 2A, B), indicating a higher tendency of the population of *S. lotanalis* to increase from this point. During the first life cycle, *S. lotanalis* had a low mortality in the egg and larval phases, showing two periods of decline in the survival rate curve: the first period was during the 1st instar, and the second period was in the beginning of the 5th instar. At the beginning of the adult phase, 75% of individuals were alive, and in this phase there was little decline in the survival at beginning and an abrupt decline in end (Fig. 2A). In the second life cycle, the survival rate curve (l_x) abruptly dropped after the eggs hatched, and this mortality was due to eggs failing to hatch. The second drop occurred from the end of the second instar to the beginning of the fourth instar and, after this, there was a stable period until the adult phase, when individuals began to die at the 98th day (Fig. 2B).

Periods of the highest mortality were during the first life cycle at the end of the egg phase. In the second life cycle, they were at the end of egg phase and from the end of the second instar to the end of the third instar (Fig. 3A, B).

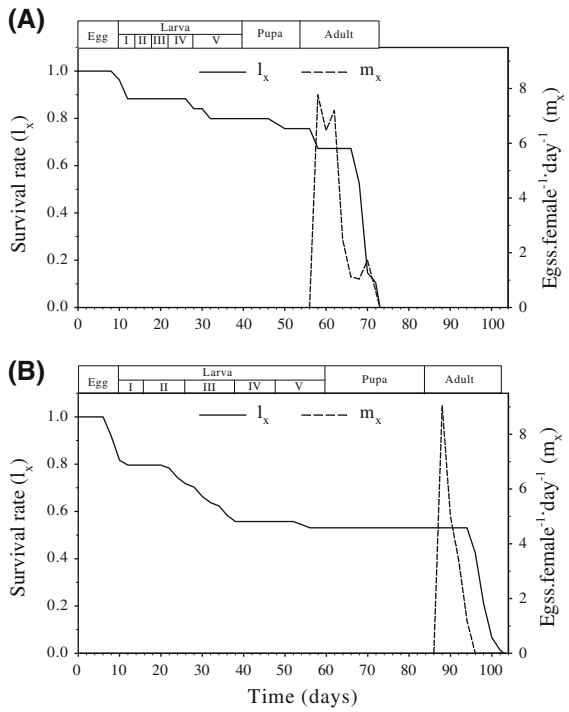

Fig. 2 Survival rate (l_x) and number of eggs female^{-1} day^{-1} (m_x) of *Salbia lotanalis* in the first life cycle (**A**) and the second life cycle (**B**), 2005–2006

Impact study

Results of the repeated-measures ANOVA show that *M. calvescens* seedlings subjected to the three levels of defoliation had significant differences in their leaf

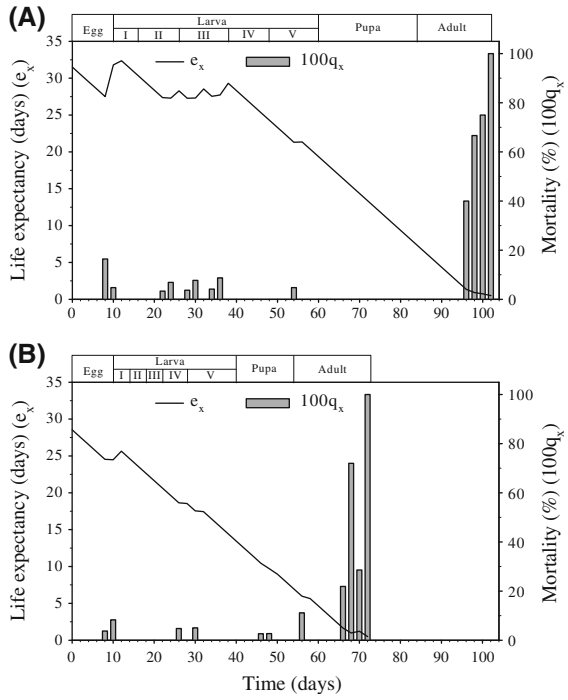

Fig. 3 Life expectancy (e_x) and mortality ($100q_x$) of *Salbia lotanalis* of first life cycle (18.7 ± 0.3°C, relative humidity 86.6 ± 1.0% and photoperiod 10.8 ± 0.01 h light) (**A**) and of second life cycle (18.7 ± 0.3°C, relative humidity 81.3 ± 1.0% and photoperiod 11.3 ± 0.05 h light) (**B**), 2005–2006

area ($F = 8.47$; d.f. = 2, 12; $P = 0.0035$) and leaf number ($F = 4.55$; d.f. = 2, 12; $P = 0.0285$). Interaction with the treatments and the time had significance for leaf number/seedling ($F = 4.81$; d.f. = 2, 24; $P < 0.0001$) and height seedlings ($F = 5.86$; d.f. = 2, 24; $P = 0.0043$). Treatment and the interaction with the treatments and the time had not significance for differences in distance between nodes ($F = 1.54$; d.f. = 2, 12; $P = 0.2470$; $F = 2.15$; d.f. = 2, 24; $P = 0.0702$, respectively) (Table 2).

According to the Bonferroni *t*-test, the leaf area and the height were higher in seedlings not defoliated by caterpillars. However, no difference was detected between seedlings subjected to 30% and 80% of defoliation (Bonferroni *t*-test: Leaf area: $t = 174.72$, d.f = 2, $P < 0.05$; Height: $t = 5.99$, d.f = 2, $P < 0.05$). The leaf number differed in seedlings subjected to the three levels of defoliation (Bonferroni *t*-test: $t = 2.41$, d.f. = 2; $P < 0.05$).

Table 2 Results of repeated-measures ANOVA of *Miconia calvescens* seedlings subjected to 0, 30 and 80% of defoliation by *Salbia lotanalis* caterpillars

Variation sources	*F*	d.f.	*P*
Leaf area (cm^2)/seedling			
Treatments	8.47	2	0.0035
Blocks	3.13	3	0.0571
Error		15	
Time	7.43	12	0.0002
Time × treatments	1.94	24	0.0816
Time × blocks	1.61	36	0.1263
Error (time)		180	
Leaf number/seedling			
Treatments	4.55	2	0.0285
Blocks	0.27	3	0.8479
Error		15	
Time	6.38	12	<0.0001
Time × treatments	4.81	24	<0.0001
Time × blocks	1.28	36	0.2032
Error (time)		180	
Height seedling (cm)			
Treatments	2.26	2	0.1391
Blocks	4.06	3	0.0270
Error		15	
Time	132.97	12	<0.0001
Time × treatments	5.86	24	0.0043
Time × blocks	3.35	36	0.0242
Error (time)		180	
Distance between nodes			
Treatments	1.54	2	0.2470
Blocks	6.22	3	0.0059
Error		15	
Time	80.44	12	<0.0001
Time × treatments	2.15	24	0.0702
Time × blocks	2.74	36	0.0142
Error (time)		180	

Discussion

Biological studies of *S. lotanalis* indicated that this species can be raised under laboratory conditions with high population growth rates. Mass-rearing is an important point for biological control, since before introduction of these agents, quarantine studies are necessary. High values of gross reproductive rate (GRR) and low values of generation time (T) also demonstrated that *S. lotanalis* has the potential for

substantial population growth, indicating that it would be possible to obtain six generations a year under optimal conditions. These characteristics are a great advantage for this biological control agent, because such a large number of generations within a short period of time would probably allow for a fast population growth in the field.

Information on reproductive value (V_x) and the intersection point of the fertility (m_x) and survival rate (l_x) curves are important for choosing the best age of female for introduction during implementation of a biological control program. The best age for introduction will be when *S. lotanalis* has the largest potential reproductive rate, and in this case the right stage would be young females. Introduction would be best accomplished by releasing gravid females of *S. lotanalis* at a precise time in their life cycle, rather than flooding the environment with a large number of individuals of indeterminate age. This inoculative approach is likely to have a larger impact on *M. calvescens*.

Impact studies of biological agents give an idea of their efficiency (Baars 2003). In this study, for example, *M. calvescens* plants that experienced high levels of defoliation by *S. lotanalis* caterpillars have their development affected because of the decrease in photosynthetic area. Furthermore, plants which suffered defoliation did not recover easily over time, and their growth rates were lower than those not defoliated (Fig. 4A–C).

A decreased foliage area of a particular exotic weed can affect interspecific competition imposed on native plants, a major problem provoked by weeds in tropical forests (Kennedy et al. 2002; Levine et al. 2004). Defoliation of invasive weeds increases light penetration through canopy and allows germination of less competitive native plants. Light and water can be the main factor limiting the development of plants (Townsend et al. 2008). Defoliation of invasive weeds can, besides decreasing light interception and consequently the shade over other plants, also reduce competition for water, allowing growth of native plants together with the weed. Attack by phytophagous insects can decrease the competitive ability of weeds compared to indigenous plants (Blossey and Notzold 1995; Zhu and Sang 2008). Meyer et al. (2007) verified that defoliation up to 35% in *M. calvescens* by the fungus *C. gloeosporioides* f.sp. *miconiae* favoured the recruitment of native

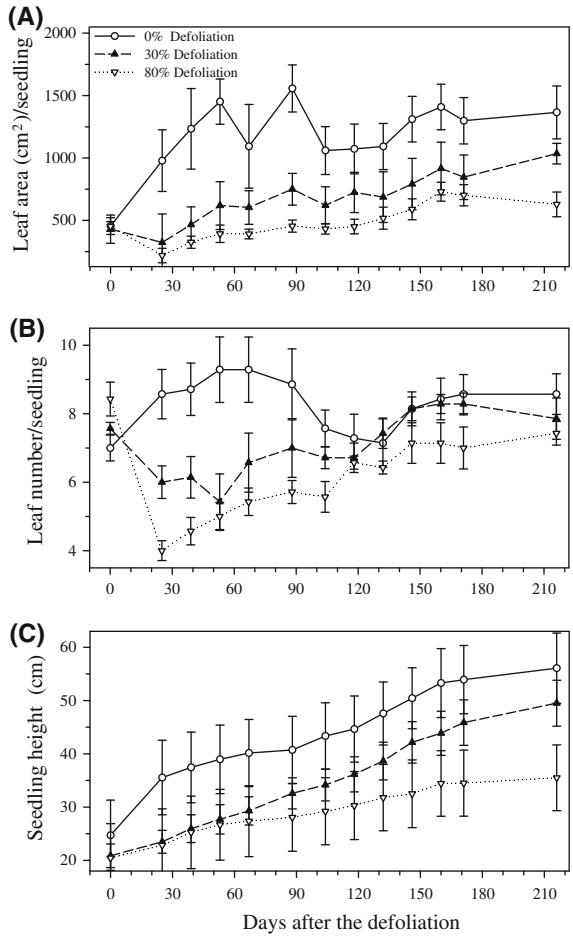

Fig. 4 Leaf area (**A**), leaf number (**B**) and seedling height (**C**) of *Miconia calvescens* seedlings subjected to three defoliation levels by *Salbia lotanalis* caterpillars, 2006, Viçosa, Minas Gerais, Brazil. Vertical lines represent the standard error of the mean

plants, including rare threatened endemic plants, by enhancing the light availability in the understory. Introduction of new biocontrol agent, like *S. lotanalis*, can decrease the ability of *M. calvescens* competition with native plants.

The impact of *S. lotanalis* on *M. calvescens* seedlings is desirable, since mature plants produce a large amount of seeds which is the main dispersal form of this weed (Medeiros et al. 1997; Meyer 1998) and the control in this phase can be not effective. The biological performance of *S. lotanalis,* as revealed by this study, the relatively ease of mass-rearing this insect species and the observed impact it is capable of causing on *M. calvescens* plants are indications that this species has a high potential as a biological agent.

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References

Baars JR (2003) Geographic range, impact, and parasitism of lepidopteran species associated with the invasive weed *Lantana camara* in South Africa. Biol Control 28:293–301

Badenes-Perez FR, Johnson MT (2007a) Ecology and impact of *Allorhogas* sp (Hymenoptera: Braconidae) and *Apion* sp (Coleoptera: Curculionoidea) on fruits of *Miconia calvescens* DC (Melastomataceae) in Brazil. Biol Control 43:317–322

Badenes-Perez FR, Johnson MT (2007b) Ecology, host specificity and impact of *Atomacera petroa* Smith (Hymenoptera: Argidae) on *Miconia calvescens* DC (Melastomataceae). Biol Control 43:95–101

Badenes-Perez FR, Johnson MT (2008) Biology, herbivory, and host specificity of *Antiblemma leucocyma* (Lepidoptera: Noctuidae) on *Miconia calvescens* DC. (Melastomataceae) in Brazil. Biocontrol Sci Techn 18:183–192

Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. J Ecol 83:887–889

Burckhardt D, Hanson P, Madrigal L (2005) *Diclidophlebia lucens*, n. sp (Hemiptera: Psyllidae) from Costa Rica, a potential control agent of *Miconia calvescens* (Melastomataceae) in Hawaii. Proc Entomol Soc Wash 107:741–749

Burckhardt D, Morais EGF, Picanço MC (2006) *Diclidophlebia smithi* sp. n., a new species of jumping plant-lice (Hemiptera, Psylloidea) from Brazil associated with *Miconia calvescens* (Melastomataceae). Mitt Schweiz Entomol Ges 79:241–250

Butt BA, Cantu E (1962) Sex determination of lepidopterous pupae. United States Department of Agriculture, Agricultural Research Service Report, pp 33–75

Csurhes SM (1997) *Miconia calvescens*, a potentially invasive plant in Australia's tropical and sub-tropical rainforests. In: Meyer JY, Smith CW (eds) Proceedings of the first regional conference on miconia control, Papeete Tahiti. Gouvernement de Polynésie française, University of Hawaii at Manoa, Centre ORSTOM, pp 72–77

Daly HV (1985) Insect morphometrics. Annu Rev Entomol 30:415–438

Denoth M, Frid L, Myers JH (2002) Multiple agents in biological control: improving the odds? Biol Control 24: 20–30

Dhileepan K, Snow EL, Rafter MA, Trevino M, McCarthy J, Senaratne K (2007) The leaf-tying moth *Hypocosmia pyrochroma* (Lep., Pyralidae), a host-specific biological control agent for cat's claw creeper *Macfadyena unguiscati* (Bignoniaceae) in Australia. J Appl Entomol 131: 564–568

Goolsby JA, Zonneveld R, Bourne A (2004) Prerelease assessment of impact on biomass production of an invasive weed, *Lygodium microphyllum* (Lygodiaceae: Pteridophyta), by a potential biological control agent, *Florocarus perrepae* (Acariformes: Eriophyidae). Environ Entomol 33:997–1002

Harley KLS, Forno IW (1992) Biological control of weeds: a handbook for practitioners and students. Inkata Press, Brisbane

Julien MH (1997) Success, and failure, in biological control of weeds. In: Julien MH, White G (eds) Biological control of weeds: theory and practical application. Australian Centre for International Ag. Research, Canberra, pp 9–15

Kaiser BA (2006) Economic impacts of non-indigenous species: *Miconia* and the Hawaiian economy. Euphytica 148: 135–150

Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636–638

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7: 975–989

Louda SM, Pemberton RW, Johnson MT, Follett PA (2003) Nontarget effects—the Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annu Rev Entomol 48:365–396

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species a selection from the global invasive species database. The Invasive Species Specialist Group (ISSG) a Specialist Group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), p 12

Medeiros AC, Loope LL, Conant P, McElvaney S (1997) Status, ecology, and management of the invasive plant, *Miconia calvescens* DC (Melastomataceae) in the Hawaiian Islands. Bishop Mus Occas Pap 48:23–36

Meyer JY (1996) Status of *Miconia calvescens* (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). Pac Sci 50:66–76

Meyer JY (1998) Observations on the reproductive biology of *Miconia calvescens* DC (Melastomataceae), an alien invasive tree on the island of Tahiti (South Pacific Ocean). Biotropica 30:609–624

Meyer JY, Florence J (1996) Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC. (Melastomataceae). J Biogeogr 23:775–781

Meyer JY, Duplouy A, Taputuarai R (2007) Dynamique des populations de l'arbre endémique *Myrsine longifolia* (Myrsinacées) dans les forêts de Tahiti (Polynésie française) envahies par *Miconia calvescens* (Melastomatacées) après introduction d'un champignon pathogène de lutte

biologique: premières investigations. Revue d'Ecologie (Terre Vie) 62:17–33

Meyer JY, Taputuarai R, Killgore E (2008) Dissemination and impacts of the fungal pathogen *Colletotrichum gloeosporioides* f.sp. miconiae (Deuteromycetinae) on the invasive alien tree *Miconia calvescens* (Melastomataceae) in the rainforests of Tahiti (French Polynesia, South Pacific). In: Julien MH, Sforza R, Bon MC, Evans HC, Hatcher PE, Hinz HL, Rector BG (eds) Proceedings of the XII international symposium on biological control of weeds, CAB International, Wallingford, pp 594–600

Murphy HT, Hardesty BD, Fletcher CS, Metcalfe DJ, Westcott DA, Brooks SJ (2008) Predicting dispersal and recruitment of *Miconia calvescens* (Melastomataceae) in Australian tropical rainforests. Biol Invas 10:925–936

Ostermeyer N, Grace BS (2007) Establishment, distribution and abundance of *Mimosa pigra* biological control agents in northern Australia: implications for biological control. BioControl 52:703–720

Picanço MC, Barreto RW, Fidelis EG, Semeão AA, Rosado JF, Moreno SC, Barros EC, Silva GA, Johnson T (2005) Biological Control of *Miconia calvescens* by phytophagous arthropods. Pacific Cooperative Studies Unit, at Manoa, Manoa. University of Hawai'i, Manoa, p 30

Price PW (1997) Insect ecology. John Wiley & Sons, New York, p 639

Raghu S, Dhileepan K (2005) The value of simulating herbivory in selecting effective weed biological control agents. Biol Control 34:265–273

Seixas CDS, Barreto RW, Matsuoka K (2002) First report of a phytoplasma-associated witches broom disease of *Miconia calvescens* in Brazil. Plant Pathol 51:801

Seixas CDS, Barreto RW, Freitas LG, Maffia LA, Monteiro FT (2004) *Ditylenchus drepanocercus* (Nematoda), a potential biological control agent for *Miconia calvescens* (Melastomataceae): host-specificity and epidemiology. Biol Control 31:29–37

Seixas CDS, Barreto RW, Killgore E (2007) Fungal pathogens of *Miconia calvescens* (Melastomataceae) from Brazil, with reference to classical biological control. Mycologia 99:99–111

Smith CW (2002) Forest pest biological control program in Hawaii. In: Smith CW, Denslow J and Hight S (eds) Proceedings of workshop on biological control of native ecosystems in Hawai'i. Pacific Cooperative Studies Unit, University of Hawaii at Manoa, Department of Botany, Honolulu, p 122

Southwood TRE, Henderson PA (2000) Ecological methods, with particular reference to the study of insect populations. Blackwell Science, Oxford, p 575

Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. Trends Ecol Evol 14:179–185

Townsend CR, Begon M, Harper JL (2008) Essentials of ecology. Blackwell Publishing, London, p 532

Williams HE, Madire LG (2008) Biology, host range and varietal preference of the leaf-feeding geometrid, *Leptostales ignifera*, a potential biocontrol agent for *Lantana camara* in South Africa, under laboratory conditions. BioControl 53:957–969

Zhu L, Sang WG (2008) Effects of defoliation on competitive interactions between invasive crofton weed (*Eupatorium adenophorum*) and its native neighbors: implication for biocontrol. Weed Sci 56:112–118

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