

**Biology, herbivory, and host specificity of *Antiblemma leucocyma*
(Lepidoptera: Noctuidae) on *Miconia calvescens* DC.
(Melastomataceae) in Brazil**

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(Received 17 October 2007; final version received 11 December 2007)

Miconia calvescens DC. (Melastomataceae) is an invasive tree considered one of the greatest threats to natural ecosystems of Hawaii and other Pacific islands. The potential for using the defoliator *Antiblemma leucocyma* (Lepidoptera: Noctuidae) as a biological control agent of *M. calvescens* was evaluated in the native habitat of the insect in Brazil. Impact assessment in the field showed that 37.2% of leaves presented damage by *A. leucocyma*, and among damaged leaves, 1.5–51.9% of the leaf area (16.3% on average) was affected. Damage was found in young to fully expanded leaves (28–915 cm² in area). Individual *A. leucocyma* developing as third through sixth instars in the laboratory consumed an average of 1348 cm² of *M. calvescens* leaf material in about 11 days. Populations of *A. leucocyma* in the field were heavily impacted (up to 83% parasitism) by a braconid parasitoid. Observations in the field and single- and two-host choice tests in the laboratory indicated that *A. leucocyma* has a narrow host range restricted to *M. calvescens*. Usefulness of this herbivore for biological control in Hawaii appears low, however, because of its probable susceptibility to generalist parasitoids.

Keywords: biological control; biotic interference; leaf area; host specificity; population dynamics; weed management

Introduction

The velvet tree, *Miconia calvescens* DC. (Melastomataceae), is a small neotropical tree considered a serious threat to natural ecosystems in Hawaii and other Pacific islands because of its ability to invade intact forests of these islands, having already displaced over 65% of the native forest in Tahiti (Meyer and Florence 1996; Medeiros, Loope, Conant and McElvaney 1997; Meyer 1998). Herbicidal and mechanical removal are the main methods used to contain the spread of *M. calvescens*, but control is difficult and costly, especially in remote areas (Medeiros et al. 1997; Kaiser 2006). Biological control is considered an essential tool for long-term management of *M. calvescens* (Smith 2002). Classical biological control of weeds via the introduction of natural enemies from the native habitat of the weed is

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one of the most important methods to manage alien invasive weeds (Julien and Griffiths 1998; Denslow and Johnson 2006). Pre-release studies in the native habitat of the invasive weed can be challenging to conduct, yet are fundamental to assess the potential of biological control agents (Goolsby, van Klinken and Palmer 2006).

In exploratory expeditions conducted to find natural enemies of *M. calvescens* in Brazil, Costa Rica, and Trinidad, larvae of *Antiblemma* spp. were often found feeding on *M. calvescens* leaves (Burkhart 1995; Picanço et al. 2005). Like *M. calvescens*, *Antiblemma* spp. (Lepidoptera: Noctuidae) are native to the neotropics (Poole 1989). One species of *Antiblemma*, *A. acclinalis* Hübner, was introduced from Trinidad to Hawaii in 1995 for biological control of *Clidemia hirta* (L.) D. Don. (Melastomataceae) (Burkhart 1987; Conant 2002). The biology and behavior of *Antiblemma* spp. is relatively unknown and *A. acclinalis* is the only species of *Antiblemma* sp. whose biology appears described in the literature (Burkhart 1984, 1987).

The objective of this study was to evaluate the biology, population dynamics, and host specificity of *Antiblemma leucocyma* Hampson in Brazil to assess its potential as a biological control agent of *M. calvescens*.

Materials and methods

This study was conducted at a field site with a native population of *M. calvescens* plants in Dionisio, in the state of Minas Gerais, in southeastern Brazil's Planalto Central, a region noted for tropical climate and hilly terrain. Dionisio is located at latitude 19°50'34"S and longitude 42°46'36"W with an elevation of 345 m above sea level. The field site was in secondary Atlantic forest heavily disturbed by adjacent eucalyptus plantations. The area sampled was approximately 1.5 ha and contained more than 50 *M. calvescens* plants ranging from immature trees less than 1 m high to mature trees about 8 m high. Distance between *M. calvescens* plants varied from a few meters, with foliage of adjacent trees overlapping, to about 150 m.

Laboratory studies were conducted in Viçosa, in the state of Minas Gerais, Brazil, on the campus of the Universidade Federal de Viçosa. During the period of this study, April to September 2006, the laboratory experienced a photoperiod of approximately 11–12:13–12 h light:dark, $22 \pm 8^\circ\text{C}$ and $80 \pm 10\%$ RH.

Insect abundance in the natural habitat

A total of 20 *M. calvescens* plants were randomly selected every 4 weeks from April to September 2006 in order to determine number of *A. leucocyma* larvae per *M. calvescens* plant at the field site. Whole plants were inspected and when this was not possible because of the location and/or size of the plant, a minimum of one-third of the plant was examined. A correction factor was applied to calculate density of larvae per plant according to the approximate proportion of each plant sampled (e.g., if only 50% of a plant could be inspected, the total number of larvae for the plant was determined as those in the 50% inspected multiplied by two).

Biology of *A. leucocyma*

Inspection of *M. calvescens* leaves and stems in the field during the surveys of insect abundance described above aimed to locate eggs, larvae, pupae and adults of *A. leucocyma* in natural conditions. To study the life cycle of *A. leucocyma* and determine defoliation of *M. calvescens* by known instars of *A. leucocyma* larvae, larvae collected from the field from April to August were placed individually in plastic rearing containers (30 × 15 × 10 cm) with one medium-sized, fully-expanded *M. calvescens* leaf, adaxial side facing upwards. Each larva was transferred to a fresh leaf every 48 h. Survival of first and second instars was very low in rearing containers, so larvae could only be studied in the laboratory starting with the third instar. A total of 15 larvae were followed from third instar to pupation by making observations every 24 h. Adult moths preserved as voucher specimens were deposited in the Zoology Museum of the Department of Biology at the University of Costa Rica.

Parasitism

In May 2006, when densities of *A. leucocyma* larvae were relatively high, a total of 30 second to fifth instars were collected from the field to assess parasitism. Larvae were reared individually in plastic containers, as described above, and observed every 24 h to assess their behaviour and check for the emergence of parasitoids.

Impact of *A. leucocyma* on *M. calvescens*

Larvae of *A. leucocyma* fed on *M. calvescens* leaves making holes of irregular shape that were generally different from leaf damage caused by other herbivores present at the time of the study, mainly *Atomacera petroa* Smith (Hymenoptera: Argidae) (Badenes-Perez and Johnson 2007b) and *Colletotrichum gloeosporioides* (Penz.) Sacc. f. sp. *miconiae* (Killgore, Sugiyama, and Barreto 1997). However, extensive defoliation of *M. calvescens* by the leaf roller *Salvia lotanalis* Druce (Lepidoptera: Pyralidae) prevented analysis of herbivory by *A. leucocyma* after June 2006. In the survey of insect abundance (description above) conducted in May 2006, damage caused by *A. leucocyma* larvae on *M. calvescens* leaves was measured by counting the total number of leaves with and without damage by *A. leucocyma* to determine the percentage of leaves per plant affected (approximately one-third of the branches of each plant examined). Among the leaves with *A. leucocyma* damage, three leaves were randomly selected per plant (a total of 60 leaves), pressed flat, and photographed with a digital camera to allow digital analysis using WinFOLIA® leaf area analysis software (Regent Instruments Inc. 2003). In addition to measurements of damage by unknown *A. leucocyma* instars occurring in the field, leaf damage by the 15 individually laboratory-reared larvae (used to study the life cycle of *A. leucocyma*) was also quantified using WinFOLIA® (Regent Instruments Inc. 2003). Data were recorded as leaf area damaged by each larva from the third through the sixth stage (until pupation).

Host specificity

Plant species growing at the field site within a 10-m radius of five randomly selected *M. calvescens* plants with *A. leucocyma* larvae were examined for *A. leucocyma* larvae

and their feeding damage in June 2006. A minimum of three plants of each of the following species were examined: *Miconia prasina* (Sw.) DC., *Clidemia hirta* (L.) D. Don. and *Tibouchina granulosa* Cogn. (Melastomataceae); *Ricinus* sp. (Euphorbiaceae); *Desmodium* sp. (Fabaceae); *Eucalyptus* sp. (Myrtaceae); *Ficus* sp. (Moraceae); *Musa paradisiaca* L. (Musaceae); *Piper* sp. (Piperaceae); *Rubus* sp. (Rosaceae); *Coffea arabica* L. (Rubiaceae); and *Citrus* sp. (Rutaceae).

Single- and two-host choice experiments were conducted in the laboratory to compare feeding by larvae of *A. leucocyma* on a control of local *M. calvescens* versus all plant species mentioned above, as well as *M. calvescens* grown from seed collected in Hawaii (bicolored type with purple abaxial side of leaves), guava, *Psidium guajava* L. (Myrtaceae), lettuce, *Lactuca sativa* L. (Asteraceae), collards, *Brassica oleracea* L. var. *acephala* (Brassicaceae), watercress, *Nasturtium officinale* Ait. F. (Brassicaceae), and an ornamental *Hibiscus* sp. (Malvaceae). The latter five plant species were chosen because they were readily available plants of agricultural/ornamental value commonly grown in both Brazil and Hawaii and because they allowed us to evaluate host range for four additional plant families. Approximately equal quantities of leaves (in terms of total leaf area) of each plant type were placed with the adaxial side facing upwards in plastic containers 30 × 15 × 10 cm. Field-collected larvae ranging from third to sixth instars were transferred to each experimental arena where they were held individually. Leaves were examined for feeding damage 24 h later. In single-host choice experiments, larvae were placed directly on plant leaves. In two-host choice experiments, larvae were placed in the middle of the experimental arena between foliage of a test plant and the control leaf of local *M. calvescens*. All experiments were replicated three times.

Statistical analysis

Larval densities of *A. leucocyma* through time were examined using analysis of variance (ANOVA) with the PROC GLM procedure of SAS[®] (SAS Institute Inc. 2004). In order to normalize the residuals, data were transformed using a natural log($x+1$) function. Although tests of significance were based on the transformed data, only untransformed data are presented. To determine the relationship between extent of leaf damage and larval development, data were subjected to stepwise multiple regression analyses performed with the PROC REG procedure of SAS[®] (SAS Institute Inc. 2004). In all cases, when significant treatment differences were indicated by *F* tests at $P \leq 0.05$, means were separated by Fisher's Protected least significant difference (SAS Institute Inc. 2004).

Results

Insect abundance in the natural habitat

Larval densities of *A. leucocyma* varied significantly between April and September 2006 ($F = 60.30$, $df = 5, 114$, $P < 0.001$), decreasing approximately 4-fold from May to June (Figure 1). This population decline coincided with a high level of parasitism (see section on parasitism below).

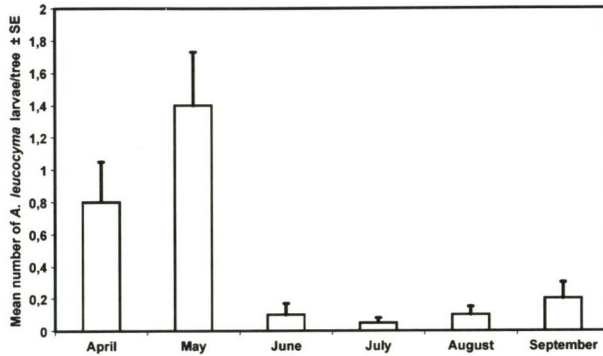


Figure 1. Abundance of *A. leucocyma* larvae on *M. calvescens* plants in their natural habitat in Dionisio, Brazil from April to September 2006.

Biology of *A. leucocyma*

White eggs were found in the field in small groups of three to eight on the abaxial side of *M. calvescens* leaves. Larvae were always found on *M. calvescens* leaves in numbers ranging from one to six larvae per tree, and never more than one larva per leaf, indicating that larvae either dispersed from their oviposition site soon after emerging from eggs or perhaps cannibalised their siblings. No pupae were found on *M. calvescens* plants with recent damage from late instars. This could indicate that under natural conditions, *A. leucocyma* larvae descend from plants to pupate in the soil or surface litter, as happens with *A. acclinalis* (Burkhart 1984). No adults were found in the field during our surveys, which were conducted in daylight. In the laboratory, observations were made starting with third instars, as all first and most second instars died soon after collection from the field and transfer to the laboratory. Based on head capsule measurements, *A. leucocyma* larvae pupated after six stages. In the laboratory, development time averaged 2.7 ± 0.2 days for the fourth stage, 3.1 ± 0.2 days for the fifth stage, and 4.1 ± 0.2 days for the sixth stage ($n = 15$). Larvae usually rested on the abaxial side of the leaf during the day, feeding mainly at night. In the laboratory, *A. leucocyma* pupated in a folded leaf of *M. calvescens*, between two leaves, or between one leaf and the surface of the plastic container-experimental arena. Pupae had a shiny brown colour and measured about 2 cm long. Of the 15 larvae followed until pupation, 11 adults emerged from the pupal case after 8–14 days and lived 7–12 days.

Parasitism

A high percentage (83%) of the 30 larvae collected appeared parasitised by an unidentified endoparasitoid species (Hymenoptera: Braconidae: Microgasterinae). Parasitised *A. leucocyma* larvae became immobile and stopped feeding 1–3 days before emergence of 6–14 parasitoid larvae per host. Parasitoids pupated around the spiracular area along the thorax and abdomen of their host. Larvae of *A. leucocyma* collected as early as the third stage were found to be parasitised. *Antiblemma leucocyma* larvae with attached parasitoid pupae were often observed in the field in May and June (F.R. Badenes-Perez, personal observation). Parasitoid adults emerging from these pupae attacked third instars of *Trichoplusia ni* (Hübner) in

the laboratory, and their larvae developed successfully to pupation, killing the host larvae within 5 days (F.R. Badenes-Perez, unpublished).

Impact of *A. leucocyma* on *M. calvescens*

Among plants sampled in May 2006, $37.2 \pm 5.2\%$ of leaves presented damage by *A. leucocyma*, with defoliation ranging from 1.5 to 51.9% (average of $16.3 \pm 1.5\%$) of the area of damaged leaves. Taking into account the average percentage of leaves with *A. leucocyma* damage per tree, the total leaf area damaged by *A. leucocyma* per tree was approximately 6.1%. Damage by *A. leucocyma* was found on young to fully expanded leaves, ranging from 28 to 915 cm² in area. An exponential function could be used to describe cumulative leaf area damaged by third through sixth instars (Figure 2). On average, one larva of *A. leucocyma* consumed 1348 ± 92 cm² of *M. calvescens* leaf area from its third stage to pupation, a period of 11.4 ± 0.4 days.

Host specificity

In the field, no *A. leucocyma* larvae were observed on plant species other than *M. calvescens*, including other Melastomataceae in the immediate vicinity of *M. calvescens* plants (Table 1). In the laboratory, *A. leucocyma* larvae fed only on *M. calvescens*, and feeding on *M. calvescens* from Brazil and Hawaii appeared to be similar (F.R. Badenes-Perez, personal observation). In spite of their usually nocturnal feeding habit, larvae exposed to non-host plants (where they did not feed for 24 h) immediately started feeding when transferred to *M. calvescens* leaves during the day.

Discussion

In its native habitat in Brazil, *A. leucocyma* caused a modest 6.1% defoliation of *M. calvescens*. This estimate at peak larval density in May appeared to represent the seasonal maximum impact of this herbivore. Other species of *Antiblemma*, *A. chiva* (Schaus) and *A. abstrusa* (Schaus) in Brazil and Costa Rica, respectively, seemed to have similar ecology and feeding behavior on *M. calvescens* as *A. leucocyma* (F.R.

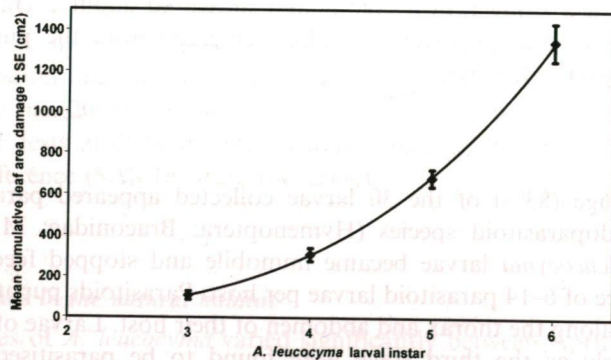


Figure 2. Cumulative leaf area damage caused by individual *A. leucocyma* larvae from third through sixth instar (until pupation) in laboratory conditions ($y = 138.34 + 1.38 e^x$, $n = 60$, $r^2 = 0.75$, $F = 166.12$, $P < 0.0001$).

Table 1. Host range of *A. leucocyma* as revealed by presence (+) or absence (-) on plant species surveyed in the field in Dionisio, Brazil, and by feeding (+) or not feeding (-) in single- and two-host choice experiments in the laboratory.

Order/Family	Species	Observed on plants in the field	Fed upon foliage in laboratory
Class Magnoliopsida-Subclass Rosidae			
Myrtales/Melastomataceae	<i>Miconia calvescens</i> DC (Brazilian monocolored type)	+	+
	<i>Miconia calvescens</i> DC (Hawaiian bicolored type)	n.t.	+
	<i>Miconia prasina</i> (Sw.) DC	-	-
	<i>Clidemia hirta</i> (L.) D. Don.	-	-
	<i>Tibouchina granulosa</i> Cogn.	-	-
Myrtales/Myrtaceae	<i>Eucalyptus</i> sp.	-	-
	<i>Psidium guajava</i> L.	n.t.	-
Rosales/Rosaceae	<i>Rubus</i> sp.	-	-
Sapindales/Rutaceae	<i>Citrus</i> sp.	-	-
Euphorbiales/Euphorbiaceae	<i>Ricinus</i> sp.	-	-
Fabales/Fabaceae	<i>Desmodium</i> sp.	-	-
Class Magnoliopsida-Subclass Asteridae			
Asterales/Lactucaceae	<i>Lactuca sativa</i> L.	n.t.	-
Rubiales/Rubiaceae	<i>Coffea arabica</i> L.	-	-
Class Magnoliopsida-Subclass Dillenidae			
Brassicales/Brassicaceae	<i>Brassica oleracea</i> L.	n.t.	-
	<i>Nasturtium officinale</i> Ait. F.	n.t.	-
Malvales/Malvaceae	<i>Hibiscus</i> sp.	n.t.	-
Class Magnoliopsida-Subclass Hamamelidae			
Urticales/Moraceae	<i>Ficus</i> sp.	-	-
Class Magnoliopsida-Subclass Magnolidae			
Piperales/Piperaceae	<i>Piper</i> sp.	-	-
Class Liliopsida-Subclass Zingiberaceae			
Zingiberales/Musaceae	<i>Musa paradisiaca</i> L.	-	-

n.t., not tested.

Badenes-Perez, personal observation). In the laboratory, feeding by individual *A. leucocyma* larvae was substantial, and this species appeared to be restricted to *M. calvescens* in the field as well as the laboratory. This combination of traits would appear to make *A. leucocyma* a suitable candidate for biological control.

The effectiveness of *A. leucocyma* as a biological control agent of *M. calvescens* outside its native range would depend on how favorable or antagonistic abiotic and biotic factors are to population growth. We measured an abrupt decline in population density of *A. leucocyma* between May and June, roughly corresponding to the beginning of the cool dry season in that part of Brazil. In areas infested by *M. calvescens* in Hawaii (Hilo and Hana), temperatures (20–27°C) and rainfall

(>2000 mm) (www.wrcc.dri.edu/) are relatively moderate and constant compared with Dionisio (Picanço et al. 2005). Therefore, climatic variation in Hawaii appears less likely to restrict *A. leucocyma* than it might in Brazil.

On the other hand, the decline in density of *A. leucocyma* at Dionisio also coincided with high parasitism by a single endoparasitoid species. Escape from this natural enemy in an area of introduction would be expected to allow *A. leucocyma* to increase to much higher population densities that might strongly impact their host plant. Unfortunately, in Hawaii a variety of parasitoids have been introduced in the past for biological control of lepidopteran agricultural pests, including noctuids (Funasaki, Lai, Nakahara, Beardsley and Ota 1988; Julien and Griffiths 1998). Some of these parasitoids are broad generalists that have been found attacking not only targeted pests but also native lepidopterans and other non-target species (Howarth 1991; Henneman and Memmott 2001; Johnson, Follett, Taylor, and Jones 2005). Widespread declines of native Hawaiian Lepidoptera over the last century, attributed to accidentally and purposefully introduced enemies (Zimmerman 1978; Gagne and Howarth 1985), support the generalisation that many lepidopterans, particularly exposed feeders such as *A. leucocyma*, have little chance of being effective biocontrol agents in Hawaii. There are no specific reports on parasitism of congeneric *A. acclinalis*, introduced to Hawaii for biological control of *C. hirta*, but this agent and its damage are rarely observed even at former release sites, which may indicate that *A. acclinalis* is subject to strong biotic interference (Conant 2002). Other noctuids released for biocontrol of *Lantana camara* L. (Verbenaceae) in Hawaii appear to have contributed significantly to control, but also have been subject to interference from parasitoids (Davis, Yoshioka and Kageler 1992). Although it remains untested whether *A. leucocyma* and the other *Antiblemma* spp. found attacking *M. calvescens* would be hindered by generalist parasitoids already established where *M. calvescens* has invaded, the prospects for biotic interference with these agents in Hawaii appear high. For this reason, a variety of other insect herbivores, including leaf, stem and fruit feeders, are considered a higher priority for biological control of *M. calvescens* in Hawaii (Burckhardt, Hanson and Madrigal 2005; Badenes-Perez and Johnson 2007a,b; Chacón 2007; Reichert 2007; Badenes-Perez, Alfaro-Alpizar, Castillo-Castillo and Johnson, in press).

Acknowledgements

We thank Drs Robert Barreto and Marcelo Picanço as well as people working in their laboratory groups at the Universidade Federal de Viçosa for assistance conducting this study. We also thank Dr Vítor Becker, at the Reserva Serra Bonita, Brazil, Dr Paul Hanson at the Universidad de Costa Rica, and Dr Isidro Chacón at the Instituto Nacional de Biodiversidad, Costa Rica, for help with insect identification. Funding was provided by the Hawaii Invasive Species Council and the US Forest Service International Programs.

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