

SPATIAL AND TEMPORAL OCCURRENCE OF BEET ARMYWORM (LEPIDOPTERA: NOCTUIDAE) MOTHS IN MISSISSIPPI

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ABSTRACT

Throughout 1994-2000, adult beet armyworm, *Spodoptera exigua* (Hübner) populations were monitored in the delta and hill regions of Mississippi using pheromone traps. Significant differences in the mean number of moths trapped were found among different geographical areas of the state. A trend was observed where the greatest number of moths was found in the Mississippi Delta, located in the western region of the state. The lowest number of moths was found in the hills located in the eastern region of the state. An annual profile of beet armyworm populations in the western section of the Mississippi Delta also revealed that wide-scale immigration of this pest typically begins at 200 Julian days (mid-July). This date could be used as a benchmark to determine when and if population levels are high enough to have the potential to cause economic damage to crops in the Mississippi Delta.

Key Words: *Spodoptera*, migration, movement

RESUMEN

A través de los años 1994 a 2000, se realizaron un monitoreo de las poblaciones de adultos del gusano trozador de la remolacha, *Spodoptera exigua* (Hübner) en las regiones de la Delta y las colinas del Estado de Mississippi usando trampas de feromonas. Se encontraron diferencias significativas en el número promedio de la polillas atrapada entre las áreas geográficas diferentes del Estado. Se observó un patrón donde se encontró el número más alto de las polillas en la Delta del Mississippi, ubicada en la región occidental del Estado. Se encontró el número de polillas más bajo en las colinas ubicadas en la región oriental del Estado. Un perfil anual de la población del gusano trozador de la remolacha en la sección occidental del Delta del Mississippi también reveló que una inmigración de amplia escala de esta plaga típicamente empieza a los 200 días Julianos (en medio de julio). Esta fecha puede ser utilizada como un estándar o norma para determinar cuando y si el nivel de la población es suficiente alto para tener el potencial de causar daño económico a los cultivos del Delta del Mississippi.

The beet armyworm, *Spodoptera exigua* (Hübner), is an occasional but serious pest of various vegetable and row crops in the mid-southern United States of America. This Old-World species was first documented in the state of Mississippi in 1920 (Mitchell 1979). Compared to other North American armyworm species (e.g., the fall armyworm, *Spodoptera frugiperda* (J. E. Smith)), knowledge of the ecology of this pest in the Mid-South is limited. Although this pest has no known photoperiod or temperature induced diapause mechanism (Kim & Kim 1997), it is able to overwinter by continuous generations in southern Florida and Texas. Therefore, initial populations of beet armyworms found throughout the state of Mississippi are believed to be the result of immigration from those areas. Hendricks et al. (1995) profiled populations of beet armyworms in the lower Mississippi Delta and noted that moths were found in all months, but the greatest num-

bers were found in the fall months (September and October). However, in that study, populations were only monitored for one season and consequently conclusions concerning population structure were limited. The purpose of this study was to examine the occurrence of beet armyworm moths across different geographical regions of Mississippi and to profile yearly moth populations to better understand the ecology of this pest in the Mid-South.

MATERIALS AND METHODS

Adult populations of beet armyworms were monitored throughout agricultural areas of Mississippi using pheromone traps. Reusable bucket style traps (Gempler's™) were baited routinely with synthetic pheromones and traps were checked weekly as described by Hendricks et al. (1995).

The primary objective of this study was to examine the population structure of beet armyworms across different geographical regions of Mississippi. An extensive trap line was conducted from 1995-1996, and 1998-2000. Traps were located in 51 counties across the state. For each year, traps were typically run between 100 and 300 Julian days. Geographical regions of the state were separated into 5 groups (W. Delta, 5 counties; C. Delta, 10 counties; E. Delta, 13 counties; C. Hills, 9 counties; NE. Hills, 14 counties) (Fig. 1). For comparisons among groups, Julian dates were separated into periods of 30 d, with the exception being the first time period which was increased to 60 d to increase numerical entries for analysis. Across multiple years and counties, cumulative mean numbers of moths trapped per time period were generated for each group. Differences among the groups were analyzed using PROC MIXED (SAS Institute 2001). Furthermore, cumulative means for the entire time period (117-326 d) were separated using the LSMEANS option of PROC MIXED (Littrell et al. 1996).

A secondary objective was to examine the seasonal profile of beet armyworms in the Mississippi Delta by using an additional data set. A continuation of a one-year survey described in Hendricks et al. (1995) was conducted. Traps (15)

were run continuously (i.e., 365 d, 12 mo, 7 y) from 1994-2000 in Washington Co., W. Delta, Mississippi. A scatter plot of the data was generated using the graphics option of SAS Analyst (SAS Institute 2001), and a 2nd-order polynomial equation that described the majority of the data (190-350 d) also was generated using simple regression (SAS Institute 2001).

RESULTS AND DISCUSSION

Throughout the agricultural areas of Mississippi, a strong trend existed where the highest population density of beet armyworm moths was located in the West Delta near the Mississippi River (Fig. 2). Between 117 and 206 Julian days, there were no significant differences ($P > 0.05$) in the cumulative mean numbers of moths trapped between the 5 geographical regions (117-176 d: $F = 2.16, P = 0.089$; 117-206 d: $F = 1.69, P = 0.169$). The fact that the beet armyworm has no known obligatory diapause (Mitchell 1979) could explain why low numbers of moths were trapped so early in the year (i.e., before wide-scale migration from southern latitudes). However, as the growing season progressed, there were significant differences ($P < 0.05$) in the cumulative mean numbers of moths trapped between the 5 geographical regions (117-236 d: $F = 3.44, P = 0.015$; 117-266 d: $F = 9.49, P < 0.001$; 117-296 d: $F = 13.28, P < 0.001$; 117-326 d: $F = 12.78, P < 0.001$). In addition, mean comparison between the 5 geographical regions showed that the population of moths found in the West Delta (i.e., the area closest to the Mississippi River) was significantly higher than populations found in all other areas (Table 1). The beet armyworm overwinters by continuous generations in southern latitudes (e.g., Florida, Texas, Caribbean, and Central America) (Mitchell 1979) and these populations probably invade Missis-

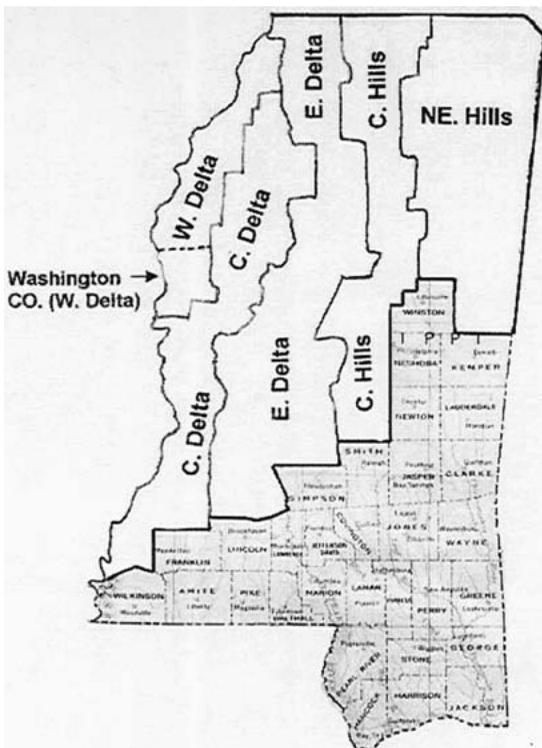


Fig. 1. Geographical regions of Mississippi monitored or BAW moth populations.

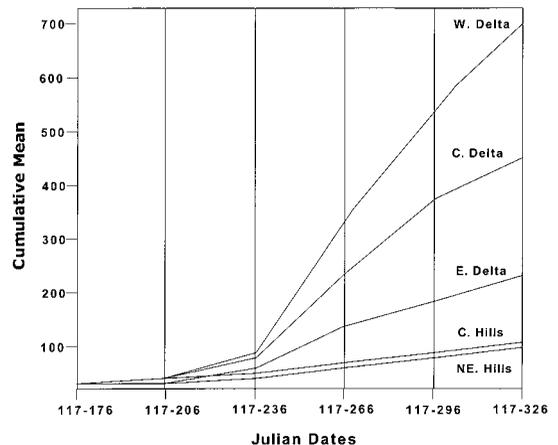


Fig. 2. Number of beet armyworm moths found in different geographical regions of Mississippi.

TABLE 1. NUMBER OF BAW TRAPPED THROUGHOUT THE 1995-1996, 1998-2000 GROWING SEASON FROM VARIOUS GEOGRAPHICAL REGIONS OF MISSISSIPPI.

Group ¹	Cumulative Mean ² ± SE
W. Delta	733.98 ± 91.92 a
C. Delta	450.54 ± 65.00 b
E. Delta	204.89 ± 57.01 c
C. Hills	101.62 ± 68.52 c
NE. Hills	82.62 ± 57.01 c
df	4, 45
F value	12.78
(P > F) ANOVA	<0.01

Means in a column followed by the same letter are not significantly different ($\alpha = 0.05$; LSMEANS option of PROC MIXED, SAS Institute 2001).

¹See Figure 1 for geographical map of Mississippi.

²Between 117-326 Julian days.

ssippi (Todd 1975; Mitchell 1979). It seems likely that seasonal weather patterns including wind currents and atmospheric disturbances from the south-central U.S. (Muller 1985; Johnson 1995;

Westbrook et al. 1995) could influence the distribution of migratory beet armyworm moths across the different geographical regions of Mississippi. Furthermore, even though this pest feeds on numerous hosts (>50) (Mitchell 1979), it is possible that differences in the population density of local and migratory moths are due to differences in larval host range and abundance among the different geographical regions of Mississippi.

The robust seasonal distribution pattern of beet armyworm moths in the Mississippi Delta suggests that the general time for wide-scale migration of this highly vagile pest may be predicted in most years (Fig. 3). Although moths were caught in all months, numbers were very low until approximately 200 Julian days. Hendricks et al. (1995) suggested that beet armyworm pupae could overwinter in the Mississippi Delta; however, without a photoperiod or temperature induced mechanism, pupal diapause seems unlikely. A more plausible explanation is that during mild winters, populations of beet armyworm larvae are able to survive and develop into pupae by feeding on wild-hosts that survive freezing temperatures in the Mississippi Delta (JJA, unpublished). In addition, Kim & Kim (1997)

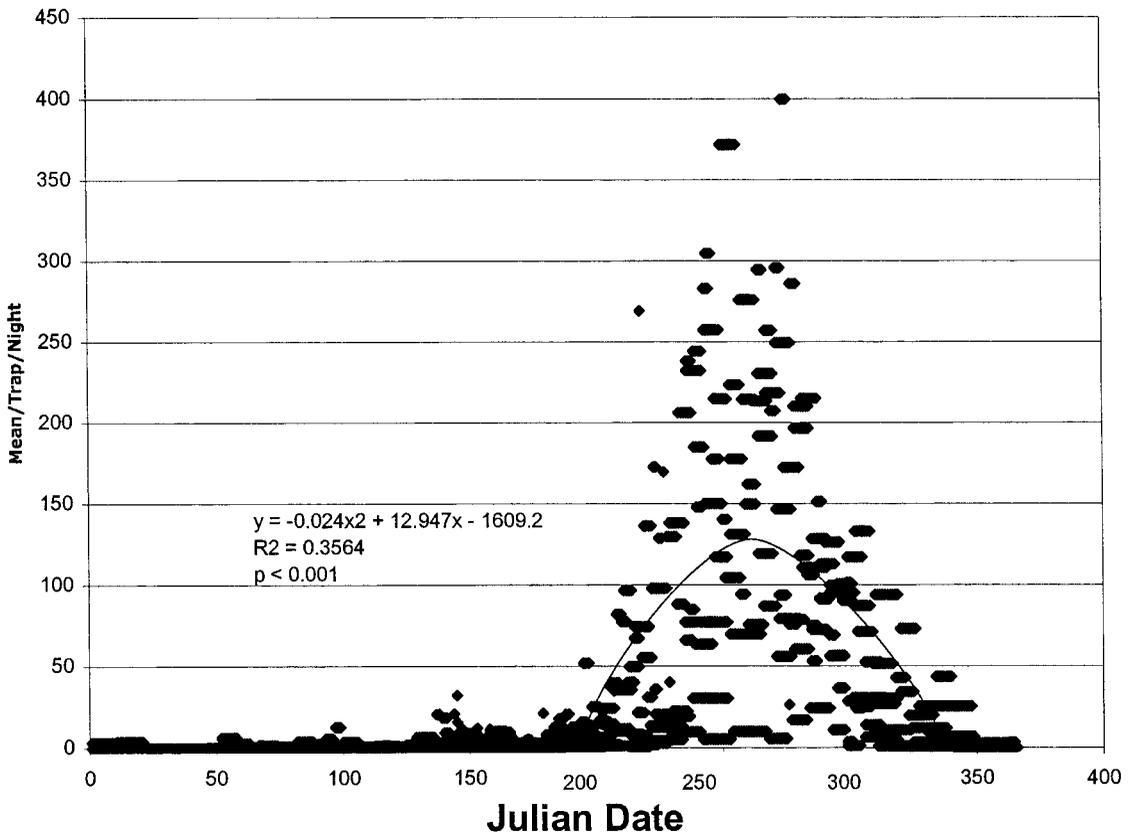


Fig. 3. Distribution of beet armyworm moths throughout Washington Co., W. Delta, Mississippi.

showed that all life-stages of beet armyworms are able to survive periods of subzero temperatures due to an efficient supercooling capacity. Therefore, low numbers of moths caught during the winter months are probably from local populations of larvae feeding on fall hosts (JJA, unpublished). The contribution and influence of this winter population on the summer and fall populations needs to be further investigated.

The seasonal distribution curve indicates a predictable period when beet armyworm migrants are likely to be an economic threat to local crops in the Mississippi Delta. Moth populations in the Mississippi Delta also were monitored in 2001, but very low levels of moths were caught in traps, and the bell-shaped curve was not apparent (data not shown). Consequently, infestations of larvae on local crops and wild-hosts were virtually non-existent throughout the year in the Mississippi Delta. Thus, it may be advantageous for consultants, growers, and researchers to begin monitoring populations of beet armyworms at 200 Julian days (mid-July) to predict if this serious pest will be numerous enough during the season to cause economic damage to crops in the Mississippi Delta.

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INFLUENCE OF HERBIVORE-DAMAGED CORN AND COTTON IN THE FIELD RECRUITMENT OF BRACONID PARASITOIDS FROM FERAL POPULATIONS

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ABSTRACT

The potential to increase parasitism by *Cotesia marginiventris* through response to chemical signals emitted by herbivore-damaged plants was investigated in corn and cotton field plots. Recruitment of feral *C. marginiventris* adult females was measured by increased parasitism. *Spodoptera frugiperda* larvae placed in the field plots and then recollected experienced a mean rate of parasitism of approximately 4-6%. Mean total mortality of the collected larvae ranged from 13 to 20%. We found no significant difference in the level of parasitism, or larval mortality between field plots containing herbivore-damaged plants and plants that were undamaged. Under the conditions of this study, we found no evidence that systemic host plant volatiles induced by herbivore feeding were used by feral *C. marginiventris* to improve foraging and parasitism at specific sites within a field of corn or cotton.

Key Words: corn, cotton, *Cotesia marginiventris*, *Spodoptera frugiperda*, parasitism

RESUMEN

El potencial para el aumentar el parasitismo por *Cotesia marginiventris* por medio de su respuesta a señales químicas emitidas por plantas dañadas por herbívoros fué investigada en parcelas de campos de maíz y algodón. El reclutamiento de hembras adultas salvajes de *C. marginiventris* fué medido por el aumento del parasitismo. Larvas de *Spodoptera frugiperda* puestas en parcelas del campo y después recolectadas, experimentaron un promedio de la tasa de parasitismo de aproximadamente 4-6%. El promedio de la mortalidad total de las larvas recolectadas fué de 13 a 20%. No encontramos ningún diferencia significativa en el nivel de parasitismo, o de la mortalidad larvaria entre las parcelas del campo que tenían plantas dañadas por herbívoros y plantas no dañadas. Bajo las condiciones de este estudio, no encontramos ningún evidencia que los volátiles sistémicos de las plantas hospederas inducidos por la alimentación de herbívoros fueron usados por los *C. marginiventris* salvajes para mejorar el forraje y el parasitismo en sitios específicos dentro de un campo de maíz o algodón.

Following the Boll Weevil Eradication Program the beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), emerged as the most important threat to cotton production over large areas of the southeastern United States (Haney et al. 1996). Other important hosts of beet armyworms include corn, tomatoes, alfalfa, onions, asparagus, potatoes, and citrus as well as numerous non-economic species (Hendricks et al. 1995). Prior to 1991, repeated outbreaks of *S. exigua* occurred regularly in Georgia and elsewhere, e.g., 1977, 1980, 1981, 1988, and 1990 (Douce & McPherson 1991).

The threat of the fall armyworm, *S. frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), to cotton production also has increased (Riley et al. 1997). Historically, fall armyworms have not been an important problem to cotton production. Instead, they have been associated with corn, sorghum, and coastal Bermuda grass (Metcalf et al. 1951). In corn production alone, fall armyworms have been responsible for losses of \$30- to 60-million annually to corn production (Sparks 1979, 1986).

Additional environmental costs also have accrued due to management programs that emphasize insecticides (Riggin et al. 1994).

Often, less than 0.1% of pesticides applied to crops reach their target (Pimentel & Levitan 1986); the remainder can affect beneficial insects and biological control agents (Pimentel et al. 1980; Ripper 1956). For instance, *Cotesia* (= *Apanteles*) *marginiventris* (Cresson) (Hymenoptera: Braconidae) is an endoparasitoid native to the southeastern United States (Ashley 1979). It has a broad host range comprising a variety of taxa in the Lepidoptera (Tingle et al. 1978), and it is considered important to the management of armyworms (Loke et al. 1983; Lewis & Nordlund 1980; Ashley 1979). Tillman & Scott (1997) reported susceptibility of *C. marginiventris* adults to commonly applied rates of selected insecticides, including acephate, azinphosmethyl, bifenthrin, cyhalothrin, cypermethrin, endosulfan, esfenvalerate, fipronil, methomyl, methyl parathion, oxamyl, profenofos or thiodicarb. This vulnerability has inspired the continued pursuit of manage-

ment tactics that either minimize or alternate insecticides in order to conserve natural enemies like *C. marginiventris* (Loke et al. 1983, Lewis & Nordlund 1980).

Several studies have demonstrated that parasitoids can use factors liberated from the food plant of their hosts as a method of locating a potential host habitat (Vinson 1975). Many investigators (Cortesero et al. 1997; Loughrin et al. 1994; Turlings & Tumlinson 1992; Turlings et al. 1991; Turlings et al. 1990; Loke et al. 1983) have reported that corn and cotton plants on which armyworms feed are attractive to *C. marginiventris* adult females in laboratory experiments. Organic volatiles from such plants emitted approximately 18-24 h after commencement of feeding by beet armyworms and released on a diurnal cycle have been implicated in this attraction (Turlings et al. 1990; Turlings et al. 1991; Turlings & Tumlinson 1992; Loughrin et al. 1994; Cortesero et al. 1997). An elicitor in the oral secretion from beet armyworms induces systematic production and emission of the attractants from plants (Alborn et al. 1997). Tumlinson et al. (1993) suggested that biological control may benefit from the use of plant breeding or genetic engineering to produce strains of plants that generate greater amounts of the herbivore-induced plant attractants.

Many aspects of this chemically-mediated tritrophic relationship have been studied in laboratory, wind tunnel experiments, including the influence of herbivore-induced plant volatiles on different host-foraging strategies of *C. marginiventris* and on another more host-specific parasitoid *Microplitis croceipes* (Cresson) (Cortesero et al. 1997). However, no data have been published concerning a fundamental aspect of this chemically-mediated tritrophic relationship, which is the attraction and increased performance of *C. marginiventris* females in the field by plants experiencing armyworm herbivory. Herein, we investigate the influence of herbivore-damaged corn and cotton plants on the recruitment of feral *C. marginiventris* adult females as measured by increased parasitism. Implications for management of armyworms are discussed.

MATERIALS AND METHODS

Insect Rearing

Spodoptera frugiperda and *S. exigua* were obtained from laboratory colonies at the USDA, ARS Crop Protection and Management Research Unit laboratory, Tifton, GA. Larvae were reared in plastic cups (30 ml) containing meridic diet (Burton 1969) at a photoperiod of 14:10 (L:D) h and temperature of $28 \pm 1^\circ\text{C}$, respectively, according to the methods of Perkins (1979) unless indicated otherwise.

Experimental Design

Experiments were conducted at the USDA-ARS-CPMRU research farm in Tifton, GA, using areas (0.7-1.0 ha) planted in corn (*Zea mays* L., cv, Pioneer 3167) and cotton (*Gossypium hirsutum* L., cv, Deltapine 90). Three trials conducted in corn (4-6 leaf stage) were initiated on 5/8/00, 5/22/00, and 6/29/00, and two trials conducted in cotton (50-75 cm high) were initiated on 6/12/00 and 6/19/00. The field plot design was the same for all trials. Sixty sites were established in a field plot. Each site consisted of a designated center plant and four sentinel plants. Two of the sentinel plants were positioned 1m on each side of the center plant within the same row. The other two sentinel plants were positioned on each side of the center plant in the adjacent rows (≈ 1 m). A randomized complete block design was used for the sites within a field plot. There were six blocks separated by ≈ 7 m with 10 sites per block. Sites in each block were separated by ≈ 8 m. Treated and control sites (5 of each) were randomly assigned for each block.

For treated sites, six 2nd to 3rd instar *S. exigua* were placed on a leaf of each center plant. Larvae were confined on a leaf in feeding disks (between a pair of ventilated plastic soft-drink lids held together by three curl clips) as described by Cortesero et al. (1997). The design was modified in the present experiment. Instead of lining the perimeter of the inside face of the lid with polystyrene foam, cotton batting was used to prevent escape of larvae without inhibiting transpiration by the leaf. Also, instead of covering holes cut in the soft-drink lids with mesh, soft-drink lids were stippled with a pin to permit free exchange of air (Fig. 1).

In trials involving corn plots, larvae were placed on the center plants at 7:00 PM, EDST, and removed from the center plants two days later (at 7:00 PM, EDST) at which time most of the leaf within the feeding disks had been consumed. Feeding disks (and larvae and larval frass) were removed by excising the leaf with a pair of scissors adjacent to the feeding disk but proximal to the plant stalk. Feeding disks also were placed on the center plants in the control sites and excised in a similar fashion, however, the feeding disks contained no larvae.

Following the removal of all feeding disks, center plants and sentinel plants in all sites (both treated and control) were infested with FAW neonates using a 'bazooka' (Wiseman et al. 1980) calibrated to deliver 20 neonates to the whorl. All center and sentinel plants were collected after 36 h (7:00 AM, EDST) and all larvae were removed and placed on meridic diet in individual 30-ml plastic cups. Larval mortality and parasitism were recorded. Similar methods were used in trials involving cotton plants with the following



Fig. 1. Cage used to contain *Spodoptera exigua* larvae and resulting frass on corn or cotton leaves (cotton shown here) during herbivory trials (see text for description). Feeding damage can be observed through the perforated side of the cage. Cage was constructed of a pair of breathable plastic soft-drink lids, with the inside perimeter lined with cotton batting, held together by three curl clips.

exceptions: (1) feeding disks (with and without larvae) were placed on the center plants at 1:00 PM and removed two days later at 6:00 AM; (2) after removal of feeding disks, center and sentinel plants were infested with FAW neonates (6:00 AM) and were collected from the field the same day at 6:00 PM.

Statistical Analysis

Data collected from corn and cotton field trials were analyzed using analysis of variance, with trial, field design block, treatment, trial/treatment interaction, and block/treatment interaction as sources of variation (PROC ANOVA & PROC GLM) (SAS Institute 1989). Number of larvae collected from the center plants and the sentinel plants, total number of larvae collected, number of plants with parasitized larvae, number of center plants with parasitized larvae, total number of parasitized larvae, and total larval mortality were the dependant variables. When significant ($P \leq 0.05$) interactions were detected between trial and treatment or between block and treatment, these interactions were tested as an error term. When significant ($P \leq 0.05$) differences were indicated, means were separated by the Tukey-Kramer statistic or paired *t*-test at $P = 0.05$.

RESULTS AND DISCUSSION

Combining data from all trials, which included field plots comprised of a center corn plant that was undamaged (control) or damaged (treated) by herbivore feeding prior to artificial infestation with larvae and four adjacent (sentinel) plants, a total of 5,921 *S. frugiperda* (FAW) larvae were collected. These larvae represent 32.9% of all larvae ($\approx 18,000$) with which plants were artificially infested. Of the 5,921 larvae recovered, 2,637 were from field plots comprised of a center plant damaged by herbivore feeding prior to artificial infestation and 2,225 larvae were collected from field plots comprised of a center plant undamaged prior to artificial infestation. The mean (\pm S.D.) percentage of larvae collected from center plants in the treated plots (19.97 ± 10.6) was not significantly different from the mean percentage of larvae collected from center plants in the control plots (20.10 ± 10.5) (Table 1).

All of the parasitoids reared from *S. frugiperda* larvae collected from the corn plots were *C. marginiventris*. The mean (\pm S.D.) percent parasitism of all *S. frugiperda* larvae collected from treated plots (4.45 ± 11.3) and control plots (5.74 ± 12.9) was not significantly different. Likewise, there was no significant difference between the mean (\pm S.D.) percent parasitism of *S. frugiperda* larvae collected from sentinel plants in treated plots (5.55 ± 11.3) and control plots (4.43 ± 7.7). The mean (\pm S.D.) percent parasitism of larvae collected from the center plants of each plot was significantly ($F = 11.58$; $df = 2, 35$; $P = 0.0009$) greater for Trial 3 (10.80 ± 17.7) than for Trial 1 (1.56 ± 4.6) or Trial 2 (2.7 ± 7.2). However, differences between treated and control field plots with respect to the mean percent parasitism of larvae collected from the center plants were not significant (Table 1). Number of plants from which parasitized larvae were recovered, percent mortality (excluding parasitism) of recovered larvae, and percent mortality (including parasitism) of recovered larvae (Table 1) were not significantly influenced by herbivore feeding on the center corn plant in the treated plots prior to larval infestation.

Trials conducted in cotton plots yielded results similar to those conducted in corn plots except the number of larvae recovered from cotton was less than the number of larvae recovered from corn. A total of 730 *S. frugiperda* larvae were collected from artificially-infested cotton plants in field plots comprised of a center plant that was undamaged (control) or damaged (treated) by herbivore feeding prior to larval infestation, and four adjacent (sentinel) plants. These 730 larvae represent a recovery of 6.1% of the total number ($\approx 12,000$) of larvae used to infest the plants in the two trials. 343 larvae were collected from field plots containing a center plant that was damaged by herbivore feeding prior to larval infestation, and 387 larvae

TABLE 1. NUMBER, LOCATION, PARASITISM AND MORTALITY OF *SPODOPTERA FRUGIPERDA* LARVAE COLLECTED FROM ARTIFICIALLY-INFESTED CORN PLANTS IN FIELD PLOTS CONTAINING A CENTER PLANT THAT WAS UNDA- MAGED (CONTROL) OR DAMAGED BY HERBIVORE FEEDING PRIOR TO LARVAL INFESTATION, AND FOUR ADJACENT (SEN- TINEL) PLANTS.

	Mean \pm S.D. ¹	
	Corn plots with herbivore- damaged center plant	Corn plots with undamaged center plant
Total number of larvae collected	2637	2225
% of collected larvae found on center plants	19.97 \pm 10.6 a	20.10 \pm 10.5 a
% parasitism of all larvae collected	5.66 \pm 10.8 a	4.80 \pm 8.0 a
% parasitism of larvae on sentinel plants	5.55 \pm 11.3 a	4.43 \pm 7.7 a
% parasitism of larvae on center plant in trial 1	1.87 \pm 5.0 a	1.26 \pm 4.2 a
% parasitism of larvae on center plant in trial 2	4.42 \pm 9.3 a	0.99 \pm 3.7 a
% parasitism of larvae on center plant in trial 3	6.98 \pm 16.2 a	14.50 \pm 18.4 a
% of plants with a parasitized larva	17.78 \pm 26.6 a	18.00 \pm 26.1 a
% mortality of collected larvae (excluding parasitism)	14.79 \pm 11.5 a	15.30 \pm 10.5 a
% total mortality of collected larvae (including parasitism)	20.45 \pm 15.5 a	20.11 \pm 11.4 a

¹Means in each row followed by the same letter are not significantly different (Tukey-Kramer test, $P < 0.05$).

were collected from field plots containing a center plant that was undamaged prior to larval infestation. Mean (\pm S.D.) percent larvae collected from center plants in the treated plots (21.96 \pm 15.9) was not significantly different from mean percent larvae collected from center plants in the control plots (25.53 \pm 17.3) (Table 2).

Similar to the trials conducted in the corn plots, all of the parasitoids reared from *S. frugiperda* larvae collected from the cotton plots were *C. marginiventris*. There was no significant difference between mean (\pm S.D.) percent parasitism of all *S. frugiperda* larvae collected from treated cotton plots (3.47 \pm 5.0) and control cotton plots (5.92 \pm 7.5). Likewise, there was no significant difference

between mean (\pm S.D.) percent parasitism of *S. frugiperda* larvae collected from sentinel plants in treated plots (3.69 \pm 5.7) and control plots (6.06 \pm 8.8). Mean (\pm S.D.) percent parasitism of larvae collected from the center plants of each plot was significantly ($F = 5.14$; $df = 1, 23$; $P = 0.0468$) greater for Trial 1 (6.40 \pm 10.9) than for Trial 2 (2.12 \pm 9.8). However, differences between treated and control field plots with respect to mean percent parasitism of larvae collected from the center plants were not significant (Table 2). Herbivore feeding on the center cotton plant in the treated plots prior to larval infestation did not significantly affect the number of plants from which parasitized larvae were collected, the percent

TABLE 2. NUMBER, LOCATION, PARASITISM AND MORTALITY OF *SPODOPTERA FRUGIPERDA* LARVAE COLLECTED FROM ARTIFICIALLY-INFESTED COTTON PLANTS IN FIELD PLOTS CONTAINING A CENTER PLANT THAT WAS UNDA- MAGED (CONTROL) OR DAMAGED BY HERBIVORE FEEDING PRIOR TO LARVAL INFESTATION, AND FOUR ADJACENT (SENTINEL) PLANTS.

	Mean \pm S.D. ¹	
	Cotton plots with herbivore- damaged center plant	Cotton plots with undamaged center plant
Total number of larvae collected	343	387
% of collected larvae found on center plants	21.96 \pm 15.9 a	25.53 \pm 17.3 a
% parasitism of all larvae collected	3.47 \pm 5.0 a	5.92 \pm 7.5 a
% parasitism of larvae on sentinel plants	3.69 \pm 5.7 a	6.06 \pm 8.8 a
% parasitism of larvae on center plant in trial 1	4.65 \pm 10.1 a	8.22 \pm 11.7 a
% parasitism of larvae on center plant in trial 2	0.57 \pm 2.7 a	3.30 \pm 12.8 a
% of plants with a parasitized larva	15.33 \pm 21.3 a	22.33 \pm 28.5 a
% mortality of collected larvae (excluding parasitism)	9.91 \pm 11.3	11.67 \pm 7.3
% total mortality of collected larvae (including parasitism)	13.38 \pm 12.4 a	17.60 \pm 10.6 a

¹Means in each row followed by the same letter are not significantly different (Tukey-Kramer test, $P < 0.05$).

mortality (excluding parasitism) of collected larvae, nor the percent mortality (including parasitism) of collected larvae (Table 2).

This study represents the first field experiments testing recruitment of *C. marginiventris* females from feral populations by herbivore-damaged corn and cotton plants. The approaches used in these field experiments are congruent with those described previously for laboratory bioassays, accommodating such important factors as time during which volatiles are released from plants (Loughrin et al. 1994; Turlings et al. 1990), time of day during which *C. marginiventris* females forage most actively and during which they have been used previously in bioassays (Turlings et al. 1991; Loughrin et al. 1994), and stage at which *S. frugiperda* larvae are preferred hosts (Loke et al. 1983; Riggin et al. 1994). Conclusions drawn previously from the results of laboratory bioassays concerning recruitment of *C. marginiventris* females by herbivore-damaged corn and cotton plants are neither confirmed nor contradicted by results of the present field study. We tested for significant difference in the level of parasitism, or larval mortality between field plots containing herbivore-damaged plants and plants that were undamaged. Under the conditions of this study, we found no evidence that systemic host plant volatiles induced by herbivore feeding were used by feral *C. marginiventris* to improve foraging and parasitism at specific sites within a field of corn or cotton.

In view of our findings, it is interesting to consider the observations made by Ruberson & Whitfield (1996) in a study of the facultative parasitization of *S. exigua* eggs by *C. marginiventris*, conducted in cotton fields where larval populations of *S. exigua* were very low. Because herbivore-induced plant attractants are lacking on plants with only egg masses present and are limited or absent in fields with low or no larval populations, they surmised that *C. marginiventris* was quite successful at locating egg masses even when foraging cues induced by larval feeding were rare. They suggested that female wasps may have been attracted to the field by the feeding of the few larvae present and then attacked the egg masses. Also, they concluded that larval damage is not the only source of cues to which *C. marginiventris* is capable of responding in close-range host location. Our results are congruent with the observations and conclusions of Ruberson & Whitfield (1996). Considering the substantial body of published work on the attractiveness of herbivore-damaged plant volatiles to foraging parasitoids and our findings that female *C. marginiventris* did not parasitize more larvae at herbivore-damaged sites than undamaged sites, we suggest that *C. marginiventris* may be attracted to the field by the herbivore-induced plant volatiles, but then rely on additional cues to locate the specific site of the host larvae.

Identifying alternative or supplemental tactics to insecticides for managing armyworms in cotton and corn continues to be a valuable pursuit. Among these tactics are biological control and host plant resistance. Tumlinson et al. (1993) suggested that biological control and host plant resistance may benefit from the use of plant breeding or genetic engineering to produce strains of plants that generate greater amounts of the herbivore-induced plant attractants. Although this tritrophic system is an interesting one with considerable support from laboratory experiments, data collected from our field study reveal that knowledge of how this tritrophic system is influenced by factors in the field is incomplete. Additional field studies are necessary before conclusions may be drawn about the potential of exploiting these herbivore-induced plant attractants to serve industry and the agricultural community.

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EFFECT OF LEAF EXTRACTS OF TEOSINTE, *ZEA DIPLOPERENNIS* L., AND A MEXICAN MAIZE VARIETY, CRIOLLO 'URUAPEÑO', ON THE GROWTH AND SURVIVAL OF THE FALL ARMYWORM (LEPIDOPTERA: NOCTUIDAE)

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ABSTRACT

The effects of leaf extracts of teosinte, *Zea diploperennis* L., and a Mexican maize variety, criollo 'Uruapeño', on the growth and survival of the fall armyworm larvae were evaluated under laboratory conditions. Hexane, methanol, and aqueous extractions were made and the extracts and residual fiber were separately incorporated into a modified Poitout & Bues meridic diet. The hexanic and methanolic extracts were concentrated in a rotary evaporator and 30 ml of each were mixed to 20 g of cellulose and then incorporated to a meridic diet. Aqueous leaf extract was not concentrated. Larval cumulative mortality, larval weight, days to pupation, pupae weight, pupae length and width, days to adult emergence were evaluated. The hexanic extract of both plants enhanced most of the FAW growth parameters. Methanolic extract and residual fiber of both plants negatively affected the pupae length and width. The aqueous extract caused 100% of larval cumulative mortality. Larvae fed on diets containing residual fiber of both plants exhibited antibiotic effects.

Key Words: *Spodoptera frugiperda*, host plant resistance, maize, corn, antibiosis

RESUMEN

Fueron evaluados los efectos de los extractos foliares del teosinte, *Zea diploperennis* L. y los de una variedad de maíz mexicano, criollo 'Uruapeño', sobre el crecimiento y sobrevivencia de larvas neonatas del gusano cogollero, bajo condiciones de laboratorio. Las extracciones se llevaron a cabo con hexano, metanol y agua, y éstas y la fibra residual sólida fueron mezclados dentro de dieta modificada de Poitout y Bues para gusano cogollero, por separado. Los extractos con hexano y metanol fueron concentrados en un rotaevaporador y 30 ml de cada uno fueron incorporados a 20 g de celulosa y luego incorporados a la dieta. La fase acuosa no fue concentrada. La mortalidad total larvaria acumulada, el peso larvario, los días a pupación, el peso de las pupas, la anchura y longitud de las pupas, y días necesitados por las pupas para alcanzar el estado adulto fueron determinados. La mayoría de los parámetros de crecimiento del gusano cogollero fueron favorecidos por la dietas con extracto hexánico de cada una de las plantas, el extracto metanólico y la fibra residual de ambas plantas afectaron negativamente la longitud y anchura de las pupas. Las dietas con el extracto acuoso tuvieron 100% de mortalidad larvaria acumulada. Las larvas alimentadas con dietas con fibra residual de ambas plantas mostraron efectos antibióticos sobre las larvas del gusano cogollero.

Translation provided by author.

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), has been recognized as a polyphagous insect and important pest of many crops, particularly maize (corn), *Zea mays* L., in the southeastern region of the United States (Luginbill 1928) and the rest of the Americas (Andrews 1988).

Over the past five decades, relatively effective and inexpensive synthetic pesticides have been extensively used to protect maize from losses caused

by FAW. There is a renewed interest in discovering new sources of plant resistance to the pests and in developing plant-derived insecticides (McMillian et al. 1967; Meisner et al. 1977; Smith & Fischer 1983; Binder & Waiss 1984; Benner 1993; Snook et al. 1997). Natural plant products can be of benefit in managing pest populations as well as providing leads for developing synthetic products with modes of action against the pests (Balandrin et al. 1985; Shapiro 1991; Benner 1993).

Resistance in maize to damage by the FAW has been extensively investigated (Wiseman 1985; Wiseman & Widstrom 1986; Wiseman et al. 1992; Wiseman et al. 1996; Davis et al. 1998; Williams et al. 2000). Some degree of natural resistance to FAW larvae is exhibited in some species of corn for example teosinte, *Zea diploperennis*, a wild perennial relative of corn, and centipede grass *Eriochloa ophiuroides*. The defense chemistry of maize and its relatives is associated with maysin, chlorogenic acid, caffeoylquinic acids, and other luteolin derivatives (Wiseman et al. 1990; Gueldner et al. 1991; Gueldner et al. 1992).

We bioassayed leaf extracts from teosinte and a Mexican maize variety, criollo 'Uruapeño', to determine their effects on the growth and survival of the fall armyworm.

MATERIALS AND METHODS

Insects

Experimental insects were from a colony derived from feral FAW larvae collected in cornfields during outbreaks in the State of Colima, México. Insects were reared on modified meridic diet for *Spodoptera frugiperda* (Poitout & Bues 1974). Neonate FAW larvae were used for all bioassays.

Teosinte and Maize Variety

Teosinte was collected in the "Reserva de la Biosfera de Manantlán", near El Terrero, Colima, México, and the Mexican maize variety, criollo 'Uruapeño', was collected in Cuauhtémoc, Colima. Plants were grown in the facilities of the Centro Universitario de Investigación y Desarrollo Agropecuario, Universidad de Colima in Tecomán, Colima using small seedbeds under nursery conditions, of $24 \pm 3^\circ\text{C}$, with a photoperiod of 16:8 (L:D), and 60-75% RH.

Stage 1 plants, exhibiting a collar of 4th leaf (Hanway 1963) were selected for the extracts. Portions of leaves, about 12 cm from the whorl, were cut, and about 50 g of leaves were macerated and used as samples for the extractions. Then to each sample, 200 ml of hexane was added, and the sample was finely ground and homogenized using a Moulinex® turbomix. Samples were incubated at 25°C for approximately 2 h with stirring at 400 rpm. The solution was filtered under vacuum using Whatman No. 1 filter paper, and the residual material was washed with 100 ml of hexane. Both filtrates were combined. Methanol (200 ml) was then used to extract the residual material using the same conditions mentioned above. Finally, the residual material was extracted with 100 ml of distilled water following the procedures mentioned above and the residual material was retained. The hexane and methanol extracts were

concentrated under reduced pressure on a rotary evaporator (Caframo model OB2000) to a final volume of 30 ml. Each was incorporated into 20 g of cellulose and air-dried. Water extracts were not concentrated but were directly added to the diet.

The hexane, methanol, and water extracts as well as the residual material (fiber) of both plants were added separately with 250 g of diet, and 10 ml of diet were dispensed into individual polystyrene cups (30 ml) ($n = 25$ cups per treatment per trial). Cups of diet were allowed to air-dry for 12 h before each cup was infested with one first instar FAW. Diets were arranged in a randomized complete block design and replicated three times. Means were separated by Student-Newman-Keuls test, $P < 0.05$. Criteria used to assess the effects of the extracts included: cumulative larval mortality, larval weight, days to prepupation and pupation, pupae weight, pupae length and width, and days required post-pupation to achieve the adult stage.

RESULTS

The weights of sixth instar and pupae were affected by the leaf extracts of *Z. diploperennis* and maize. Heavier larvae and pupae were obtained when diets containing the hexane and methanol extracts of both plants and regular diet were used. Lighter FAW larvae and pupae were obtained when fiber (residual material) diets were used (Table 1). The 6th instars that fed on diets with hexane and methanol extracts of *Z. diploperennis* were 1.86-fold and 1.56-fold heavier, respectively, than the larvae that fed on diets containing *Z. diploperennis* fiber. The weights of 6th instars and pupae reared on diets with hexane and methanol extracts of *Z. diploperennis* and the regular diet were statistically similar. Larvae that developed on diets with hexane and methanol extracts of 'Uruapeño' were 1.58 and 1.55 fold, respectively, heavier than those larvae that developed on 'Uruapeño' fiber diets. Weights of 6th instars and pupae reared on regular diet were statistically similar to those from diets supplemented with hexane and methanol extracts (Table 1). Similar effects were observed on weights of pupae from larvae reared on diets containing hexane and methanol extracts. The mean weights ranged from 191.0 mg to 211.9 mg for *Z. diploperennis*, and from 187.5 mg to 207.4 mg for 'Uruapeño' (Table 1).

Overall, FAW growth and developmental criteria were affected by leaf extracts and residual fiber. The criteria evaluated from insects reared on residual fiber diets showed extended developmental times, diminished pupae length and width, and increased cumulative larval mortality, compared with those from insects reared on diets containing hexane and methanol extracts of both plants and regular diet (Table 2).

TABLE 1. WEIGHTS OF *SPODOPTERA FRUGIPERDA* LARVAE AND PUPAE FED ON A MERIDIC DIET SUPPLEMENTED WITH LEAF EXTRACTS OF *ZEA DIPLOPERENNIS* AND A MEXICAN *Z. MAIZE* VARIETY, 'URUAPEÑO'.

Strain or variety	Extracts and diets				
	Hexane (<i>n</i>)	Methanol (<i>n</i>)	Water (<i>n</i>)	Fiber (<i>n</i>)	Regular (<i>n</i>)
	6th instar weights (mg)				
<i>Z. diploperennis</i>	407.5 a (25)	343.3 ab (21)		219.0 c (16)	373.0 a (24)
<i>Z. maize</i> var. 'Uruapeño'	322.0 a (19)	315.0 ab (24)	—	202.8 c (14)	373.0 a (24)
	Pupae weights (mg)				
<i>Z. diploperennis</i>	211.9 a (16)	191.0 a (14)	—	142.5 b (12)	198.6 a (22)
<i>Z. maize</i> var. 'Uruapeño'	207.4 a (12)	187.5 a (15)	—	149.4 b (6)	198.6 a (22)

Means in the same row followed by the same letter are not significantly different ($P < 0.05$; Student-Newman-Keuls test).

One hundred percent larval mortality was obtained when larvae were fed diets containing water extracts. Higher larval survival was obtained when larvae were fed diets containing hexane extracts of leaves from *Z. diploperennis* (100%). Lower larval mortality was obtained with the methanol extract of 'Uruapeño' and regular diet (8.3%) (Table 2). A significant reduction was observed in the FAW survival of larvae fed on fiber diets of both plants when compared with the FAW survival of larvae fed the regular diet and diets containing hexane and methanol extracts of both plants (Table 1).

DISCUSSION

Research on maize resistance to fall armyworm and corn earworm (*Helicoverpa zea* Boddie) has attempted to correlate resistance to chemistry of the plant, plant parts, or tissues. The mechanisms of non-preference, antixenosis or tolerance, and antibiosis are involved in some or all of the manifestations of plant resistance. Some effects of antibiosis in resistant crop genotypes on insects, including extended development, decreased pupal weight, and increased mortality compared with individuals reared on susceptible hosts, were described by Painter (1951). The presence of maysin, chlorogenic acid, apimaysin and 3'-methoxymaysin in leaves or silks in corn, as possible factors of resistance to the fall armyworm and corn earworm, was reported by Gueldner et al. (1992). Maysin in corn, teosinte and centipede grass also occurs naturally and is considered as a pest bioregulator (Gueldner et al. 1991).

The allelochemical activity observed among the *Z. diploperennis* and corn extracts in this study suggests that a variety of plant chemicals may have biological activities on FAW larvae, prepupae and pupae. FAW larvae reared on diets containing water extract and residual fiber were killed or were significantly lighter than those reared on diets with hexane and methanol extracts and regular diet. Differences in larval

growth and development could have caused by antibiosis as a result of the presence of maysin and its analogues (Wiseman et al. 1992; Molina-Ochoa et al. 1996), non-preference, or a combination of the two mechanisms (Williams et al. 1987). Our results are in accord with those manifestations of antibiosis observed in resistant genotypes, but we did not discount the non-preference mechanism, because it was not evaluated in this study.

We suggest that one or more non-polar compounds that enhanced the growth and development of the FAW and diminished the cumulative larval mortality may be present in the hexane fraction of both plants. In the methanol fraction of *Z. diploperennis*, the presence of polar or polar compounds affected the pupal length and width. Diets containing the aqueous fraction and fiber contained dissolved antibiotic polar compounds that negatively affected most of the growth and developmental criteria, and increased the cumulative larval mortality. The survival of larvae reared on diets containing fiber was reduced 1.84-fold, 1.46-fold, and 1.69-fold compared to survival of larvae reared on diets containing hexane and methanol extracts of *Z. diploperennis*, and regular diet, respectively. FAW survival was reduced 2.0-fold and 2.44-fold in larvae reared on fiber diets compared with larvae reared on diets containing hexane and methanol extracts of 'Uruapeño', and was reduced 2.44-fold compared with larvae reared on the regular diet, respectively. The aqueous extracts of both plants contained the antibiotic factors and reduced FAW larval survival to 0%. Larval mortality indicates that the concentration of toxic leaf factor(s) is greatly increased in extract-supplemented diets, presumably due to the removal of phago-stimulants and/or growth-promoting substances in water extracts (Smith & Fischer 1983). The higher mortality exhibited in the diets with water extracts and residual fiber of both plants indicated that both plants contained chemicals that severely reduced survival and negatively affected the growth and development of FAW larvae. Once these chemicals are removed

TABLE 2. GROWTH AND DEVELOPMENTAL CRITERIA OF *SPODOPTERA FRUGIPERDA* LARVAE FED ON MERIDIC DIET SUPPLEMENTED WITH LEAF EXTRACTS OF *ZEA DIPLOPERENNIS* AND A MEXICAN *Z. MAIZE* VARIETY, 'URUAPEÑO'.

Strain or variety	Extracts and diets				
	Hexane (n)	Methanol (n)	Water (n)	Fiber (n)	Regular (n)
	Days to prepupation				
<i>Z. diploperennis</i>	18.81 a (16)	19.80 a (15)		29.31 b (13)	18.77 a (22)
<i>Z. maize</i> var. 'Uruapeño'	18.92 a (19)	21.63 ab (24)	—	27.67 c (14)	18.77 a (22)
	Days to pupation				
<i>Z. diploperennis</i>	20.94 a (16)	21.14 a (14)		31.33 b (12)	20.77 a (22)
<i>Z. maize</i> var. 'Uruapeño'	20.67 a (12)	23.29 a (14)	—	28.0 b (6)	20.77 a (22)
	Pupal length (cm)				
<i>Z. diploperennis</i>	1.61 a (16)	1.51 b (14)		1.46 b (12)	1.64 a (22)
<i>Z. maize</i> var. 'Uruapeño'	1.61 a (12)	1.61 a (14)	—	1.48 b (6)	1.64 a (22)
	Pupal width (cm)				
<i>Z. diploperennis</i>	0.53 a (16)	0.47 ab (14)		0.43 c (12)	0.51 a (22)
<i>Z. maize</i> var. 'Uruapeño'	0.49 ab (12)	0.50 a (14)	—	0.46 c (6)	0.51 a (22)
	Days required by pupae to reach the adult stage				
<i>Z. diploperennis</i>	10.40 a (16)	11.18 a (11)	—	10.20 a (5)	11.18 a (22)
<i>Z. maize</i> var. 'Uruapeño'	11.17 a (12)	13.00 a (9)	—	11.50 a (4)	11.18 a (22)
	Cumulative larval mortality				
<i>Z. diploperennis</i>	0.0 d (24)	20.8 c(24)	100 a (24)	45.8 b (24)	8.3 c (24)
<i>Z. maize</i> var. 'Uruapeño'	25.0 c(24)	8.3 c (24)	100 a (24)	62.5 b (24)	8.3 c (24)

Means in the same row followed by the same letter are not significantly different ($P < 0.05$; Student-Newman-Keuls test).

through extraction, the larvae were able to use the nutrients contained in the leaves. The availability of these nutrients increased the survivorship to adulthood above those on the residual fiber and regular diet. Similar results were obtained by Bosio et al. (1990). Our results differ from those obtained by Quisenberry et al. (1988), because they did not find differences in mortality caused by diets containing water extracts of different varieties of Bermudagrass, *Cynodon dactylon* (L.). Their results suggested that the water extractable factors did not contribute to FAW resistance in the grasses evaluated.

The possibility of FAW management by foliar application of the plant tissue extracts of insect resistant corn varieties or its wild relatives could also be explored in greenhouse and field conditions. A knowledge of the compounds occurring in corn "criollo", improved varieties and wild relatives of corn would also facilitate the selection and aid the development of selective breeding procedures for varieties with an inherent resistance to FAW in tropical conditions.

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PATHOGENS AND PARASITIC NEMATODES ASSOCIATED
WITH POPULATIONS OF FALL ARMYWORM
(LEPIDOPTERA: NOCTUIDAE) LARVAE IN MEXICO

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ABSTRACT

Larvae of fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) and soil samples were collected in six Mexican states. Larvae were collected from whorl-stage corn, grain sorghum, forage sorghum, and Sudan grass fields in 64 locations during the summer of 2000, to determine the occurrence of entomopathogens and parasitic nematodes. A total of 5591 FAW larvae from 64 locations were examined for indigenous FAW biological control agents. Overall total larval mortality was 3.935%. The larval mortality percent due to entomopathogens and parasitic nematodes was 3.524%, other causes reached 0.411% of total mortality. Three species of entomopathogenic fungi representing two classes, Hyphomycetes (*Nomuraea rileyi*, and *Hirsutella* sp.) and Zygomycetes (*Entomophthora* sp.) were recovered from FAW larvae, and two species of Hyphomycetes (*Metarhizium anisopliae* and *Beauveria bassiana*) were isolated from soil samples. An unidentified microsporidian was recovered from four locations in the State of Jalisco, three from Michoacán, three from Nayarit, and one from Veracruz and Colima, respectively. Mermithid nematodes were recovered from 24 FAW larvae at three locations in Nayarit and three larvae were recovered from two locations in Veracruz. Six larvae showing symptoms of viral disease were collected from Sinaloa (2), Jalisco (2), Michoacán (1), and Nayarit (1). Entomopathogenic nematodes from the genus *Heterorhabditis* sp. and *Steinernema* sp. were isolated from soil samples from Colima in one and two locations, respectively. *Steinernema* sp., and *Heterorhabditis* sp. were isolated from soil in one location in Michoacán. *Steinernema* sp. was recovered from two locations of Jalisco. In this survey, *N. rileyi*, mermithid nematodes, and microsporidia were the most frequent pathogens and parasites.

Key Words: *Spodoptera frugiperda*, biological control, occurrence, survey, maize, mermithid nematodes, entomopathogenic microorganisms

RESUMEN

Larvas de gusano cogollero, *Spodoptera frugiperda* (J. E. Smith) (FAW), y muestras de suelo se colectaron de 64 localidades en seis estados mexicanos. Las larvas fueron recogidas de campos cultivados con maíz, sorgo para grano, sorgo forrajero y pasto Sudán, en estado de cogollo o verticilio, con la finalidad de determinar la presencia de entomopatógenos y nematodos parásitos, durante el verano de 2000. 5591 larvas se colectaron para buscar agentes de control biológico indígenas de esta plaga. En general la mortalidad total de larvas fue de 3.935%, la mortalidad larvaria provocada por patógenos y parásitos fue de 3.524%, otras causas provocaron 0.411%. Tres especies de hongos entomopatógenos pertenecientes a dos clases, los Hyphomycetes (*Nomuraea rileyi* e *Hirsutella* sp.) y los Zygomycetes (*Entomophthora* sp.) fueron recuperados de larvas de gusano cogollero, y dos especies de Hyphomycetes (*Metarhizium anisopliae* y *Beauveria bassiana*) fueron aislados de muestras de suelos. Un microsporidio no identificado fue recuperado en cuatro localidades de Jalisco, tres de Michoacán, tres de Nayarit, y una en Veracruz y Colima, respectivamente. Los nematodos mermítidos parasitaron a veinticuatro larvas en tres localidades de Nayarit, así mismo, a tres larvas en dos localidades de Veracruz. Las larvas con síntomas de virosis se presentaron en dos sitios de Sinaloa, dos en Jalisco, una en Michoacán y una en Nayarit. Los nematodos entomopatógenos de los géneros *Steinernema* sp. y *Heterorhabditis* sp. fueron aislados de muestras de suelo, presentándose en Colima, en una y dos localidades, respectivamente; en Michoacán ocurrieron en una localidad, respectivamente, pero *Steinernema* sp. solo se presentó en dos localidades de Jalisco. En este inventario, *N. rileyi*, los nematodos mermítidos y el microsporidio fueron los patógenos y parásitos más frecuentes.

Translation provided by author

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), causes considerable economic losses in maize, sorghum, peanuts, cotton, soy-

beans and occasionally other crops, in most of the countries of the Western Hemisphere (Sparks 1986). Control of this pest is usually achieved

through the application of synthetic insecticides (Hruska & Gould 1997), but their high cost, environmental contamination, development of resistance to chemicals, and pest resurgence (Colborn 1995; Crowe & Booty 1995) have encouraged the search for alternatives more compatible with the environment. Microbial control is an environmentally sound and a valuable alternative to the use of chemicals for controlling this pest.

Interactions between insect host, environment, insect host age (Fuxa et al. 1988; Molina-Ochoa et al. 1996), pathogens and plant to be protected (Bergman & Tingey 1979; Hamm & Wiseman 1986; Barbercheck 1993; Wiseman & Hamm 1993; Molina-Ochoa et al. 1997, 1999) determine the strategies for using pathogens in microbial control (Hamm 1984). FAW larvae are susceptible to entomopathogenic bacteria, fungi, nematodes, protozoa, and viruses (Gardner & Fuxa 1980; Agudelo-Silva 1986; Hamm et al. 1986; Patel & Habib 1988; Richter & Fuxa 1990; Lezama-Gutierrez et al. 1996; Molina-Ochoa et al. 1996; Molina-Ochoa et al. 1999). The insect host age, habitat and soil type, pesticide use, agricultural practices, and location, influence the natural distribution of biological control organisms (Croft & Brown 1975; Fuxa 1982; Agudelo-Silva 1986; Hamm et al. 1986; Sosa-Gomez & Moscardi 1994; Vanninen 1996; Chandler et al. 1997; Mietkiewski et al. 1997; Molina-Ochoa et al. 2001).

As a result of economic and environmental concerns, surveys for natural enemies of the FAW occurring in Mexico have been conducted to develop a better understanding of the pathogen complex, parasitic nematodes and parasitoids (Lezama-Gutierrez 2001, Molina-Ochoa 2001, Molina-Ochoa et al. unpublished). These two surveys conducted in four Mexican states reported the occurrence of the fungi *Beauveria bassiana*, *Nomuraea rileyi*, and *Hirsutiella* sp., an unidentified microsporidian, mermithid nematodes, and an ascovirus affecting FAW larvae. The occurrence of the bacterium *Bacillus thuringiensis* and steinernematid and heterorhabditid nematodes are reported from soil samples.

This paper reports on the presence of entomopathogens and parasitic nematodes in FAW larval populations and recovered from soil samples of corn, grain sorghum, forage sorghum, and Sudan grass fields from six Mexican states, during the summer of 2000.

MATERIALS AND METHODS

Isolation of Entomopathogens from FAW Larvae

During August and September of 2000, FAW larvae were collected from whorl-stage corn, grain and forage sorghum, and Sudan grass fields in 64 locations in the Mexican states of Sinaloa, Nayarit, Jalisco, Colima, Michoacán, and Ver-

acruz. Concurrently, four soil samples were obtained from each location in all of the states. Location 43 comprised a combination of collections from adjacent corn and grain sorghum field in whorl-stage. Sample size ranged from 33 to 119 FAW larvae per field, but most often sample size was about 90. The number collected was corrected by subtracting the number that died from injury or unknown causes during the first days after collection. Collection data and percent infection by entomopathogens and parasitic nematodes is presented in Table 1. Larval mortality due to insect parasitoids is reported elsewhere (Molina-Ochoa et al., in press).

Larvae were placed individually in 30 cc plastic cups with regular pinto bean diet (Burton & Perkins 1989) and maintained in the laboratory to record the larvae infected by entomopathogens and parasitic nematodes. Mermithid nematodes that emerged from larvae were collected and placed in crystal vials containing 2 ml of 70% ethanol. Dead FAW larvae showing signs of fungal infection were placed in plastic Petri dishes (60 × 10 mm) lined with a piece of 5.5 cm-diameter filter paper (Whatman No. 1) moistened with sterile distilled water until the fungus sporulated on the insect surface. A medium composed of 200 ml of V8 vegetable juice, 5 g glucose, 2 g yeast extract, 3 g CaCO₃, 15 g agar, and 800 ml distilled water (Fargues & Rodriguez-Rueda 1980) for isolating the fungus *Nomuraea rileyi* was used. A Sabouraud-dextrosa-agar medium enriched with 1% (w/v) yeast extract (SDAY), and 500 ppm chloramphenicol (Lezama et al. 1996) for growing other fungus species was used. Entomophthorales were not isolated.

Isolation of Entomopathogenic Fungi and Nematodes from Soil

In each location of the six surveyed states, a 2 kg combined soil sample was collected. A soil subsample, about 500 g from four different points a few meters apart, was obtained by digging to a depth of 10-15 cm with a small shovel. Soil samples were deposited into double plastic bags, tagged, stored in a plastic cooler, and taken to the laboratory where they were kept at 25°C until processing. The storage time ranged from a few days to three weeks. Soil was thoroughly mixed and passed through a 0.4 mm mesh sieve, breaking soil lumps and separating any litter.

For isolating entomopathogenic nematodes and fungi, greater wax moth (GWM) larvae, *Galleria mellonella* L., were used as bait (Bedding & Akhurst 1975; Tarasco et al. 1997). From the 2 kg combined soil sample from each location, two samples were placed in 1000 ml capacity plastic pots and five GWM last instar larvae were released into each pot. Pots were incubated at 25°C in the dark for a 10-day period (Woodring & Kaya

TABLE 1. GEOGRAPHIC LOCATION, DATE, ALTITUDE, CROP (*), SAMPLE SIZE (N), AND TOTAL PERCENT FAW LARVAE INFECTED BY ENTOMOPATHOGENS AND PARASITIC NEMATODES IN SIX MEXICAN STATES (***) DURING 2000.

Code	Date	Location	Coordinates	Altitude (m)	Crop	n	Infected larvae (%)
C1	08/04	El poblado, Coquimatlán	19°13.698'N 103°47.722'W	422	c	90	0.000
C2	08/04	Pueblo Juárez, Coquimatlán	19°10.752'N 103°54.634'W	279	c	90	2.222
C3	08/04	Amachico, Coquimatlán	19°10.667'N 103°56.351'W	328	c	90	0.000
C4	08/06	Los mezcales, Comala	19°20.811'N 103°47.639'W	608	c	90	1.111
C5	08/06	El remate, Comala	19°24.825'N 103°47.639'W	817	c	90	0.000
C6	08/06	Carrizalillo, Quesería	19°25.389'N 103°41.000'W	1550	c	90	0.000
C7	08/06	Quesería	19°23.362'N 103°34.882'W	1304	c	90	0.000
C8	08/06	Villa de Alvarez	19°17.201'N 103°47.030'W	515	c	90	0.000
C9	08/06	Juluapan, Villa de Alvarez	19°18.890'N 103°49.611'W	539	c	90	1.111
C10	08/07	Tepames, Colima	19°08.231'N 103°37.996'W	519	c	90	2.222
C11	08/07	Etapilla, Colima	19°59.549'N 103°31.140'W	304 1557	c	90	1.111
J1	08/08	Ciudad Guzmán	19°40.11'N 103°28.830'W		c	90	2.222
J2	08/15	Los pinitos, Tonila	19°25.343'N 103°32.447'W	1326	c	90	11.111
J3	08/15	Pialla, Tuxpan	19°27.293'N 103°28.514'W	1079	c	90	44.444
J4	08/15	Atenquique, Tuxpan	19°31.778'N 103°27.851'W	1338	c	90	11.111
J5	08/17	Canoas, Zapotiltic	19°34.073'N 103°27.324'W	1391	c	90	12.111
J6	08/17	Apastepe	19°38.060'N 103°30.950'W	1709	c	90	3.333
J7	08/17	Teocuitatlán	20°07.035'N 103°32.704'W	1369	c	90	1.111
J8	08/17	Zacoalco de Torres	20°11.988'N 103°33.806'W	1425	c	90	1.111
J9	08/17	Acatlán de Juárez	20°25.362'N 103°33.406'W	1575	c	96	4.166
J10	08/17	Tlajomulco de Zúñiga	20°29.396'N 103°28.298'W	1607	c	92	4.347
J11	08/18	Zapopan	20°43.129'N 103°29.041'W	1670	c	90	10.000
J12	08/18	Magdalena	20°53.008'N 103°02.509'W	1496	c	93	2.150
J13	08/23	Crucero de Magdalena	20°56.300'N 104°02.509'W	1386	c	92	9.782
M1	08/09	Totolán	19°58.890'N 102°40.183'W	1590	c	90	0.000
M2	08/09	Santa Inés Tocumbo	19°44.502'N 102°34.967'W	1630	c	90	0.000

*Corn (c), Forage Sorghum (fs), Grain Sorghum (gs), and Sudan Grass (sg).

**Colima (C), Jalisco (J), Michoacan (M), Nayarit (N), Sinaloa (S), and Veracruz (V).

TABLE 1. (CONTINUED) GEOGRAPHIC LOCATION, DATE, ALTITUDE, CROP (*), SAMPLE SIZE (N), AND TOTAL PERCENT FAW LARVAE INFECTED BY ENTOMOPATHOGENS AND PARASITIC NEMATODES IN SIX MEXICAN STATES (***) DURING 2000.

Code	Date	Location	Coordinates	Altitude (m)	Crop	n	Infected larvae (%)
M3	08/09	Peribán	19°33.106'N 102°26.586'W	1475	c	90	0.000
M4	08/10	Cointzio	19°41.609'N 101°16.398'W	1932	c	90	2.222
M5	08/10	Cerro "La Esperanza"	19°41.233'N 101°18.890'W	1998	c	90	2.222
M6	08/11	Tejabán	19°13.342'N 101°53.714'W	587	c	90	0.000
M7	08/11	Carretera a Nueva Italia	19°03.290'N 102°02.458'W	442	c	90	2.222
M8	08/11	Presa de Zicuirán	18°56.191'N 101°54.650'W	292	c	63	12.698
M9	08/11	El ceñidor, Nueva Italia	18°59.651'N 102°11.577'W	350	c	57	1.754
M10	08/12	La Guadalupe Parácuaro	19°07.472'N 102°12.519'W	540	fs	90	2.222
M11	08/12	Las yeguas Parácuaro	18°57.308'N 102°16.733'W	359	fs	90	2.222
M12	08/12	El cirrián, Nueva Italia	18°53.661'N 102°07.483'W	255	c	90	0.000
N1	08/18	Santa María del Oro	21°20.121'N 104°40.174'W	1160	c	90	2.222
N2	08/18	El rincón, Tepic	21°32.472'N 104°56.123'W	849	c	96	2.083
N3	08/18	El pichón, Tepic	21°33.479'N 104°56.937'W	774	c	95	4.210
N4	08/19	Xalisco	21°19.601'N 104°55.060'W	1042	c	107	7.476
N5	08/19	El refilión, Xalisco	21°19.407'N 104°55.323'W	964	c	90	2.222
N6	08/19	Compostela	21°17.858'N 104°54.044'W	920	c	93	21.505
N7	08/19	La presa, Compostela	21°13.714'N 104°52.162'W	928	c	90	2.222
N8	08/20	Las lumbres, Acaponeta	22°20.795'N 105°18.141'W	48	C&gs	60	13.333
N9	08/23	Seboruco	21°20.850'N 104°40.749'W	1134	c	90	2.222
N10	08/23	Ahuacatlán	21°06.331'N 104°27.427'W	1120	c	90	1.111
S1	08/21	Bacurimi, Culiacán	24°51.688'N 107°29.478'W	70	gs	97	0.000
S2	08/21	La campana, Culiacán	24°58.415'N 107°33.517'W	143	gs	100	2.000
S3	08/21	Pericos, Mocorito	25°03.574'N 107°39.547'W	80	gs	95	1.052
S4	08/21	Rancho viejo Mocorito	25°06.033'N 107°43.165'W	89	gs	98	1.020
S5	08/22	Aguapepito Mocorito	25°03.861'N 107°39.547'W	68	sg	95	1.052
S6	08/22	Comanito Mocorito	25°09.006'N 107°39.645'W	91	gs	95	0.000

*Corn (c), Forage Sorghum (fs), Grain Sorghum (gs), and Sudan Grass (sg).

**Colima (C), Jalisco (J), Michoacan (M), Nayarit (N), Sinaloa (S), and Veracruz (V).

TABLE 1. (CONTINUED) GEOGRAPHIC LOCATION, DATE, ALTITUDE, CROP (*), SAMPLE SIZE (N), AND TOTAL PERCENT FAW LARVAE INFECTED BY ENTOMOPATHOGENS AND PARASITIC NEMATODES IN SIX MEXICAN STATES (**)
DURING 2000.

Code	Date	Location	Coordinates	Altitude (m)	Crop	n	Infected larvae (%)
S7	08/22	La poma Badiraguato	25°15.749'N 107°40.739'W	157	c c	100	0.000
S8	08/22	La majada Badiraguato	25°14.076'N 107°39.781'W	145	c	92	0.000
V1	09/02	Seis de Enero, Xalapa	19°34.115'N 96°50.207'W	950	c	91	0.000
V2	09/02	Altolucero, Almolonga	19°35.063'N 96°47.384'W		c	33	6.060
V3	09/02	Actopan	19°34.623'N 96°48.589'W		c	64	1.562
V4	09/02	Los González, Actopan	19°31.894'N 96°41.294'W	432	c	113	0.884
V5	09/02	Bocana, Actopan	19°24.416'N 96°36.731'W	311	c	119	0.000
V6	09/03	El volador, Coatepec	19°21.594'N 96°51.037'W	709	c	90	3.333
V7	09/03	Palmillas	19°12.293'N 96°46.221'W	702	c	59	0.000
V8	09/03	Tierra Colorada	19°13.255'N 96°21.916'W	46	c	45	4.444
V9	09/04	Cerro gordo	19°25.252'N 96°39.566'W	443	c	45	0.000
V10	09/04	Lacumbre	19°23.320'N 96°38.807'W	366	c	66	0.000

*Corn (c), Forage Sorghum (fs), Grain Sorghum (gs), and Sudan Grass (sg).

**Colima (C), Jalisco (J), Michoacan (M), Nayarit (N), Sinaloa (S), and Veracruz (V).

1988, Bidochka et al. 1998). Larval cadavers were removed and surface-sterilized with 1% Sodium hypochlorite for a 3 minute-period, then washed three times with sterile distilled water and placed on damp filter paper in a 60 mm diameter sealed Petri dish, and incubated at 25°C for 12 days (Chandler et al. 1997). Entomopathogenic fungi from the larvae were isolated using SDAY, with 500 ppm of chloramphenicol (Lezama-Gutierrez et al. 1996). Fungi were identified by microscopic inspection of morphological characteristics *in situ* or after isolation in SDAY according to the criteria by Brady (1979) and Samson et al. (1988).

The entomopathogenic nematodes were separated to genera by identifying coloration of *Galleria* cadavers according to Woodring & Kaya (1988).

Entomopathogenic viruses and bacteria from FAW larvae and soil, respectively, have not been yet isolated or identified.

Geographical Coordinates and Collection Data

A Garmin GPS III Plus™ was used for obtaining the coordinates and altitude data. Location, date, place, coordinates, altitude, crop, sample size, and percentage of infected larvae are shown in Table 1.

RESULTS

In this survey, out of 5591 FAW larvae collected from 64 locations in six Mexican states, the entomopathogens and parasitic nematodes killed 197 larvae. Overall larval mortality percentage due to these organisms was 3.524%. Mortality percentage per location ranged from 0.000 to 44.444% (Table 1). Considering the total mortality due to entomopathogens and parasitic nematodes, 137 (69.54%) larvae were killed by entomopathogenic fungi, 26 (13.19%) larvae were killed by microsporidia, six (3.04%) larvae were killed by viruses, and 28 (14.21%) larvae were killed by mermithid nematodes. Two classes of entomopathogenic fungi were collected. The class Zygomycetes was represented by *Entomophthora* sp. which infected a larva from Colima and a larva from Veracruz. The class Hyphomycetes was represented by *Nomuraea rileyi* and *Hirsutella* sp. which infected 134 and one larvae, respectively. *N. rileyi* was responsible for 68.020% of total mortality due to entomopathogens and parasitic nematodes, and was the most abundant and widely distributed, occurring in all the states. *Hirsutella* sp. occurred in Sinaloa, only. Mermith-

ids were collected from the states of Nayarit (23), and Veracruz (5), only, and accounted for approximately 14.21% of total mortality of FAW larvae.

The 26 FAW larvae infected by microsporidia were collected in five of six states sampled (Michoacán (10), Nayarit (9), Jalisco (5), Colima (1), Veracruz (1) and Sinaloa (0)). These entomopathogens accounted for 13.19% of the total FAW larval mortality. The symptoms of larvae infected with these entomopathogens were similar to the unidentified microsporidia reported by Lezama-Gutiérrez et al. (2001). They often were dry and fragile when dead, resembling cigarette ashes. Few FAW larvae showed symptoms of ascovirus infection (Hamm et al. 1986). Two were detected in Jalisco in one location, two in two separate locations in the same municipality in Sinaloa, one in Michoacán, and one in Nayarit. The viruses were not identified by electron microscopy. The percentage of fall armyworm larvae infected by pathogens and parasitic nematodes at each location is shown in Table 2.

Entomopathogens Isolated from Soil

Two species of entomopathogenic fungi, *Metarhizium anisopliae* and *Beauveria bassiana*, were recovered from 10 of 64 soil samples. *M. anisopliae* was recovered from four of eleven locations in Colima, and in one location in each of Nayarit, Jalisco, and Michoacán. *Beauveria bassiana* was recovered from two locations in Veracruz and one in Michoacán.

Two genera of entomopathogenic nematodes, *Steinernema* sp., and *Heterorhabditis* sp. were collected from soil samples. Steinernematid nematodes were recovered from five of 64 locations (two locations in Colima, two in Jalisco, and in one in Michoacán). Heterorhabditid nematodes were recovered in two locations, one in Colima and one in Michoacán.

DISCUSSION

Current research efforts are focused on selecting native and exotic entomopathogens, which are highly virulent to arthropod pests, for developing efficient and environmentally-sound bioinsecticides. The high susceptibility of fall armyworm larvae and other lepidopterous pests to strains of *N. rileyi*, *B. bassiana* and *M. anisopliae* has been demonstrated (Bustillo & Posada 1986; Habib & Patel 1990; Lecuona & Lanteri 1999). *N. rileyi* has been reported infecting FAW larvae naturally in Brasil (Valicente 1989), Venezuela (Agudelo-Silva 1986), Puerto Rico (Pantoja et al. 1985), Colombia (Vargas & Sánchez 1983), United States (Fuxa 1982), Mexico (Lezama-Gutiérrez et al. 2001), and other countries. In this survey, *N. rileyi* caused 68.020% of the total FAW larval mortality due to pathogens and parasitic nema-

todes, and was the most abundant and widely distributed entomopathogen, occurring in each of the six states surveyed. Similar results were reported by Lezama-Gutiérrez et al. (2001) from a survey conducted in Colima, Jalisco, and Michoacán.

Entomophthora aulicae was reported attacking FAW larvae on grain sorghum in Georgia (Hamm 1980; Schwehr & Gardner 1982), and Argentina (Vera et al. 1995). *Entomophthora* sp. and *Hirsutella* sp. were reported attacking larvae of this pest with parasitism rates that ranged from 0.6% to 1.1%, respectively (Lezama-Gutiérrez et al. 2001). In this study, parasitism rates for *E.* sp., and *H.* sp. were 3.030 and 1.520%, respectively. Total FAW mortality caused by all the pathogens was 3.524% (197 larvae killed).

An unidentified microsporidian was the third cause of FAW total larval mortality with 13.19%, and was similar to that reported by Lezama-Gutiérrez et al. (2001). Most larvae infected with the microsporidian were collected from Michoacán, Nayarit, and Jalisco, with 10, 8, and 5 infected larvae, respectively. The arrangement of the spores of this microsporidian suggested that this entomopathogen was neither *Nosema* nor *Vairimorpha* as previously reported by Gardner & Fuxa (1980).

A few larvae showed symptoms and signs similar to those from ascoviruses, but the identity of these viruses was not verified by electron microscopy. Occurrence of entomopathogenic viruses has been reported in Latin America, in Puerto Rico, Argentina, Brasil, and Mexico (Valicente 1989; Pantoja & Fuxa 1992; Vera et al. 1995; Lezama-Gutiérrez et al. 2001).

In this survey, the mermithid nematodes were important natural enemies of FAW larvae. They were the second most important mortality factor, causing 14.21% of total mortality. Nematodes from the genus *Hexameris* have been reported attacking FAW larvae in Honduras, Brasil, Nicaragua, and Argentina (Van Huis 1981; Valicente 1989; Wheeler et al. 1989; Vera et al. 1995). Mermithids attacking FAW larvae in Mexico were reported by Alcocer-Gómez & Méndez-Villa (1965). They found parasitism ranging from 8 to 100% during a 3-year study. An association between the pest density and percent of parasitism was determined. Rainfall also was cited as an important factor in influencing percent parasitism. In a recent survey conducted in Mexico, mermithid nematodes caused larval mortality ranging from 0.0 to 14.9% in Colima (Lezama-Gutiérrez et al. 2001). But in our survey, mermithids were not recovered in Colima. However, similar percentages of mortalities were recorded (0.000 to 15.054%) from other locations, with the highest rate of parasitism from Nayarit and Veracruz. A possible reason for the difference between the findings of Lezama-Gutiérrez et al. (2001) and those we report is that most of the locations in Colima were

TABLE 2. PERCENTAGE OF FAW LARVAE INFECTED BY ENTOMOPATHOGENS AND MERMITHIDS AT EACH LOCATION.

Code*	<i>N. rileyi</i>	<i>Hirsut.</i>	<i>Entomoph.</i>	Mermithid	Microsporo.	Viruses
C1	0	0	0	0	0	0
C2	2.222	0	0	0	0	0
C3	0	0	0	0	0	0
C4	0	0	1.111	0	0	0
C5	0	0	0	0	0	0
C6	0	0	0	0	0	0
C7	0	0	0	0	0	0
C8	0	0	0	0	0	0
C9	1.111	0	0	0	0	0
C10	1.111	0	0	0	1.111	0
C11	1.111	0	0	0	0	0
M1	0	0	0	0	0	0
M2	0	0	0	0	0	0
M3	0	0	0	0	0	0
M4	2.222	0	0	0	0	0
M5	2.222	0	0	0	0	0
M6	0	0	0	0	0	0
M7	2.222	0	0	0	0	0
M8	0	0	0	0	12.698	0
M9	0	0	0	0	1.754	0
M10	1.111	0	0	0	1.111	0
M11	1.111	0	0	0	0	1.111
M12	0	0	0	0	0	0
J1	2.222	0	0	0	0	0
J2	8.888	0	0	0	0	2.222
J3	44.444	0	0	0	0	0
J4	11.111	0	0	0	0	0
J5	12.222	0	0	0	0	0
J6	2.222	0	0	0	1.111	0
J7	1.111	0	0	0	0	0
J8	0	0	0	0	1.111	0
J9	4.166	0	0	0	0	0
J10	4.347	0	0	0	0	0
J11	7.777	0	0	0	2.222	0
J12	2.150	0	0	0	0	0
J13	8.696	0	0	0	1.086	0
N1	0	0	0	0	2.222	0
N2	1.041	0	0	0	0	1.042
N3	3.157	0	0	0	1.053	0
N4	2.803	0	0	0	4.673	0
N5	2.222	0	0	0	0	0
N6	6.451	0	0	15.054	0	0
N7	1.111	0	0	1.111	0	0
N8	0	0	0	13.333	0	0
N9	2.222	0	0	0	0	0
N10	1.111	0	0	0	0	0
S1	0	0	0	0	0	0
S2	2.000	0	0	0	0	0
S3	0	0	0	0	0	1.052
S4	0	0	0	0	0	1.020
S5	0	1.052	0	0	0	0
S6	0	0	0	0	0	0
S7	0	0	0	0	0	0
S8	0	0	0	0	0	0

*Locations are described in Table 1.

N. rileyi = *Nomuraea rileyi*, *Hirsut.* = *Hirsutella* sp., *Entomoph.* = *Entomophthora* sp., Mermithid = mermithid nematode, Microsporo. = Microsporidia, Viruses = with virosis signs.

TABLE 2. (CONTINUED) PERCENTAGE OF FAW LARVAE INFECTED BY ENTOMOPATHOGENS AND MERMITHIDS AT EACH LOCATION.

Code*	<i>N. rileyi</i>	<i>Hirsut.</i>	<i>Entomoph.</i>	Mermithid	Microspo.	Viruses
V1	0	0	0	0	0	0
V2	3.030	0	3.030	0	0	0
V3	0	0	0	1.562	0	0
V4	0	0	0	0	0.884	0
V5	0	0	0	0	0	0
V6	0	0	0	3.333	0	0
V7	0	0	0	0	0	0
V8	2.222	0	0	2.222	0	0
V9	0	0	0	0	0	0
V10	0	0	0	0	0	0

*Locations are described in Table 1.

N. rileyi = *Nomuraea rileyi*, *Hirsut.* = *Hirsutella* sp., *Entomoph.* = *Entomophthora* sp., Mermithid = mermithid nematode, Microspo. = Microsporidia, Viruses = with virosis signs.

different than those sampled by Lezama-Gutierrez et al. (2001) during the summer of 1998.

The entomopathogenic fungi and nematodes were recovered in 26.5% of the soil samples (17 of 64 locations). *M. anisopliae* and *B. bassiana* were isolated in 15.6% of the samples. They occurred in Colima, Michoacán, Nayarit, and Veracruz, but were not found in Jalisco and Sinaloa. *M. anisopliae* was recovered from five locations in Colima, and one location each in Michoacán and Nayarit. *B. bassiana* was recovered in two locations of Veracruz and one location in Michoacán. In a study conducted in Szczecin, Poland using soils collected from forests during the spring and autumn, the entomopathogenic fungi *M. anisopliae* and *B. bassiana* infected wax moth larvae (Mietkiew-

ski et al. 1998), and *M. anisopliae* was the dominant species. Recently, Lezama-Gutierrez et al. (2001) reported three species of entomopathogenic fungi recovered from soil samples using the *Galleria* technique; *M. anisopliae*, *B. bassiana*, and *Paecilomyces fumosoroseus*, with *M. anisopliae* being the most dominant species. In our soil samples, *M. anisopliae* was also the most dominant, occurring in 10.9% of the locations, while *B. bassiana* occurred only in 4.7% of the locations (Table 3).

Steinernematid and Heterorhabditid nematodes were found in seven of 64 locations (10.9%). Steinernematid nematodes were recovered from Colima in two locations, one in Michoacán, and two in Jalisco. Heterorhabditids occurred in Colima and Michoacán, in one location, respectively. Low rates

TABLE 3. ENTOMOPATHOGENIC FUNGI (HYPHOMYCETES) AND NEMATODES (RHABDITIDA: STEINERNEMATIDAE AND HETERORHABDITIDAE) RECOVERED FROM SOIL SAMPLES IN DIFFERENT MEXICAN LOCATIONS.

Code*	Location	Entomopathogen
C2	Pueblo Juárez, Coquimatlán	<i>Heterorhabditis</i> sp.
C5	El remate	<i>Metarhizium anisopliae</i>
C5	El remate	<i>Steinernema</i> sp.
C6	Carrizalillo	<i>Steinernema</i> sp.
C6	Carrizalillo	<i>Metarhizium anisopliae</i>
C7	Quesería	<i>Metarhizium anisopliae</i>
C10	Tepames	<i>Metarhizium anisopliae</i>
J1	Ciudad Guzmán	<i>Metarhizium anisopliae</i>
M2	Santa Inés, tocumbo	<i>Metarhizium anisopliae</i>
M4	Cointzio	<i>Beauveria bassiana</i>
M6	Tejabán	<i>Steinernema</i> sp.
M7	Carretera a Nueva Italia	<i>Heterorhabditis</i> sp.
J2	Los pinitos, Tonila	<i>Steinernema</i> sp.
J3	Pialla, Tuxpan	<i>Steinernema</i> sp.
N6	Compostela	<i>Metarhizium anisopliae</i>
V8	Tierra Colorada	<i>Beauveria bassiana</i>
V9	Cerro Gordo	<i>Beauveria bassiana</i>

*Locations are described in Table 1.

of entomopathogenic nematode recovery have been reported in different regions around the world, and range from 3.9% to 21.4% (Constant et al. 1998; Tangchitsomkid et al. 1998; Griffin et al. 2000; Rosa et al. 2000; Lezama-Gutierrez et al. 2001). Soil pH and type, altitude, habitat, soil temperature, croplands, orchards, pastures, and proximity to coastal lands were discussed as possible factors affecting the occurrence of these entomopathogens.

The diversity and distribution of entomopathogens and parasitic nematodes occurring in Mexico could play an important role in regulating the FAW larval populations. Additional research is needed on the identification, biology, and potential of the microsporidia frequently recovered in the surveys conducted during 1998 and 2000. There is also a need to identify the role of mermithid nematodes as potential biological control agents. Additional research has already been conducted at the Universidad de Colima, Mexico, to identify the steinernematid and heterorhabditid nematodes isolated, and to determine their potential for biological control of fall armyworm larvae and other lepidopterous pests.

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PARASITOIDS AND PARASITES OF *SPODOPTERA FRUGIPERDA*
(LEPIDOPTERA: NOCTUIDAE) IN THE AMERICAS
AND CARIBBEAN BASIN: AN INVENTORY

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ABSTRACT

An inventory of parasitoids and parasites of fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), was conducted using references describing parasitized FAW eggs, larvae, pupae and adults collected from different crops or habitats throughout the Americas and the Caribbean Basin. The crops and countries where these parasites were reported occurring in the Americas is also inventoried. Maize was the crop where the FAW was more frequently collected followed by rice. Overall, *Chelonus insularis* (Cresson) had the broadest natural distribution in the Americas. For the North American region *C. insularis*, *Chelonus* sp., and *Euplectrus platyhypenae* (Howard) were the most relevant parasitoids. In Central America, *C. insularis* was the most prevalent parasitoid, and in the South American region the most prevalent parasites were *Archytas incertus* (Macq.), *A. marmoratus* (Tns.), *C. insularis*, and *Meteorus laphygmae* (Viereck). *Diapetimorpha introita* (Cresson) is the most important pupal parasitoid of FAW occurring mainly in North America. An acugutturid, *Noctuidonema guyanense* (Remillet & Silvain), is the most important ectoparasitic nematode attacking adults of FAW and other noctuid moths in South and Southeastern US, and Mexico in North America, Caribbean Basin, Central America, and Northern South America.

Key Words: parasitoids, fall armyworm, *Chelonus insularis*, *Diapetimorpha introita*, *Noctuidonema guyanense*, maize, natural distribution, biological control

RESUMEN

Un inventario de los parasitoides y parásitos del gusano cogollero, *Spodoptera frugiperda* (J. E. Smith) se llevó a cabo usando referencias relacionadas con parásitos de huevos, larvas, pupas y adultos del insecto plaga colectados de diferentes cultivos en su ámbito de distribución. Además, un inventario se realizó de los cultivos y países donde estos parásitos atacaron al gusano cogollero en América. La plaga fue colectada principalmente en el maíz, seguido por el arroz. *Chelonus insularis* (Cresson) fue el parasitoides distribuido más ampliamente en todo el ámbito de distribución del. *C. insularis*, *Chelonus* sp. y *Euplectrus platyhypenae* (Howard) fueron los parasitoides más prevalentes en Norteamérica. En Centroamérica, *C. insularis* fue el parasitoides más prevalente, y en la región Sudamericana lo fueron *Archytas incertus* (Macq.), *A. marmoratus* (Tns.), *C. insularis* y *Meteorus laphygmae* (Viereck). *Diapetimorpha introita* (Cresson) fue el parasitoides de pupas más importante y éste habitó en Norteamérica, principalmente. Un acugutturido, *Noctuidonema guyanense* (Remillet & Silvain) fue el nematodo ectoparásito más importante atacando adultos de gusano cogollero y otros noctuidos en el Sur y Sureste de los Estados Unidos de América y México en Norteamérica, Cuenca del Caribe, Centroamérica y Norte de Sudamérica.

Descriptores: parasitoides, gusano cogollero, *Chelonus insularis*, *Diapetimorpha introita*, *Noctuidonema guyanense*, maíz, ámbito de distribución, control biológico

Biodiversity in agro-ecosystems can be as varied as the crops, weeds, arthropods, and microorganisms themselves, and may differ according to geographical location, climate, soil, and human factors. Experimental evidence suggests that

biodiversity can be used for improved pest management (Altieri 1991). A major problem in all areas of agriculture is the lack of basic research on taxonomy of insect pests and their natural enemies. This problem is greatest in tropical coun-

tries where the needs are also greater (Claridge 1991). Waage (1991) stated that agricultural systems are generally simpler than the natural habitats from which they are developed. These systems have fewer plant species, fewer primary consumers, and generally fewer natural enemy species. In tropical systems, despite their great biodiversity, natural enemies could be particularly susceptible to local extinction as a result of habitat destruction and unfavorable cropping practices such as indiscriminate use of pesticides (Claridge 1991; Waage 1991).

More than 200 years ago, the fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), was recognized as a destructive pest of many agricultural crops (Luginbill 1928). In the continental United States the costs for chemical control and losses due to this pest exceeded \$300,000,000 during 1977 (Gross & Pair 1986). The biological control of FAW in areas of overwintering and throughout its annual geographical distribution is a highly desirable alternative to conventional control methods (Gross & Pair 1986). Luginbill (1928) and Vickery (1929) recognized the value of parasitoids in reducing larval populations of FAW. Parasitoids and parasites can be highly effective at little or no cost, serve as biotic insecticides in place of chemicals, provide long-term control without the target pest developing significant resistance to them, and impose minimal or no harm to humans or the environment (Wilson & Huffaker 1976; Stary & Pike 1999).

Sivasubramaniam et al. (1997), and Dent (2000) advocated that the first step in any investigation of the role of natural enemies in pest control should involve a field survey to determine which species are present and how their numbers vary in relation to those of the pest insects. Surveys on the FAW parasitoids and other natural enemies in different parts of its range have been conducted because of increasing economic and environmental concerns (Carrillo 1980; Ashley 1986; Castro et al. 1989; Gross & Pair 1991; Cave 1993; Lezama-Gutiérrez et al. 2001; Molina-Ochoa et al. 2001). However, information about distributions and host plants of the FAW and the accompanying parasites and parasitoids are scattered throughout the published literature, and most reviews of FAW parasitoids have emphasized those attacking the egg and larval stages (Ashley 1986). The aim of this paper is to summarize the information and provide an inventory of the known FAW parasites and parasitoids occurring in the Americas and the Caribbean, indicating the host stage attacked, the crops from which parasitized fall armyworm were collected, and the country of collection. In addition, because parasites and parasitoids of the pupal and adult stages of FAW have received little attention in most previous reviews on this subject, we provide an expanded discussion of these natural enemies.

MATERIALS AND METHODS

Sources of Information

Research was conducted to obtain information, papers, and bibliographic references reporting the collection of parasitized FAW from the field. In the US, we used the Agricola and CAB Abstracts database at the University of Nebraska-Lincoln in Lincoln, Nebraska, and the University of Georgia, Coastal Plain Experiment Station in Tifton, Georgia. We collected references cited in reviews and catalogs of FAW parasites (Guimarães 1971; Marsh 1978; Ashley 1979; Ashley 1986; Andrews 1988) to verify information concerning host plant of parasitized FAW, location of the collected FAW, and stage of FAW attacked. We also used various internet search engines to identify published reports of parasitized FAW collected from the field. In México, we collected papers from Latin American journals and proceedings from meetings of International and Mexican Entomological and Biological Control Societies. Information was also obtained from the libraries in the Facultad de Ciencias Biológicas y Agropecuarias (School of Biological, Agricultural & Animal Sciences) of the Universidad de Colima, and in the Centro Nacional de Referencia de Control Biológico (CNRCB)-Comisión Nacional de Sanidad Agropecuaria-SAGARPA (National Center for Reference on Biological Control) in Tecmán, Colima, México, during 2001 and 2002.

Organization of the Information

The classification (order, family, genus and species) of each parasite and parasitoid collected from FAW is presented in Table 1. The crop from which parasitized FAW were collected, the FAW stage attacked, the country from which parasitized FAW were collected, and the bibliographic references for each record were included in Table 1 whenever the information was available. We preferred to list only original references that report the collection of FAW from the field. Therefore, review articles that contain lists of insects collected by other authors (Guimarães 1971; Marsh 1978; Ashley 1979; Ashley 1986; Andrews 1988) usually are omitted for the entries in Table 1. Because of the quantity involved, all references listed in Table 1 were not cited in the text. Data on FAW parasitoids and parasites from Table 1 have been summarized as the number of species in each taxon reported from different geographical regions (Table 2), Number of species and FAW stage attacked reported from different countries (Table 3), and number of species in each taxon reported from FAW collected from different host plants (Table 4). Omission of pertinent literature from this paper is the authors' responsibility and was unintentional.

TABLE 1. FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
Diptera: Bombyliidae				
<i>Poecilanthrax (Anthrax) lucifer</i> (Fabricius)	L	US	BG	Allen 1921
Diptera: Phoridae				
<i>Megaselia</i> sp.	L	Honduras Nicaragua	(N/G) M	Cave 1993 Maes 1989
Diptera: Sarcophagidae				
<i>Helicobia morionella</i> (Aldrich)	L	Honduras Nicaragua	(N/G) M	Cave 1993 Maes 1989
Syn: <i>Sarcophaga morionella</i> Aldrich				
<i>Rivinia assidua</i> (Walker)	L	US	(N/G)	Luginbill 1928
Syn: <i>Sarcophaga assidua</i> (Walker)				
<i>Sarcophaga georgiana</i> (Weideman)	L	US	M	Dew 1913
<i>Sarcophaga lambens</i> (Weideman)	L	Lesser Antilles	M	Fennah 1947
<i>Sarcophaga</i> sp.	L	US Venezuela	(N/G) (N/G)	Enkerlin 1975 Terán 1974
<i>Sarcodexia sternodontis</i> (Townsend)	L	Honduras	M	Maes 1989; Cave 1993
Diptera: Tachinidae				
<i>Tachinidae</i> sp.	L	Mexico Nicaragua	M,S M	Lacayo 1977 Ryder & Pulgar 1969; Ashley 1986
<i>Acroglossa vetula</i> (Reinhard)	L	Brazil Honduras Venezuela	(N/G) (N/G) M	Guimarães 1977 Cave 1993 Notz 1972
Syn: <i>Spallanzania vetula</i> (Reinhard)				
<i>Admontia degeerioides</i> (Coquillett)	L	US	(N/G)	Luginbill 1928
<i>Archytas analis</i> Fabricius	L	Argentina Barbados Honduras Mexico Nicaragua US Venezuela	M M M,R,O,T M M (N/G) (N/G)	Virla et al. 1999 Alam 1979 Cave 1993 Ravlin & Stehr 1984 Maes 1989 Luginbill 1928 Terán 1974
<i>Archytas apicifer</i> (Walker)	L	US	(N/G)	Ravlin & Stehr 1984
<i>Archytas incasana</i> Townsend	L	Argentina Brazil Chile Venezuela	M (N/G) M (N/G)	Virla et al. 1999 Guimarães 1977 Etcheverry 1957 Terán 1974
Syn: <i>Archytas divisus</i> (Walker)				

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference		
<i>Archytas incertus</i> (Macquart)	L	Argentina	M	Virla et al. 1999		
			SY	Molinari & Avalos 1997		
			(N/G)	Parker et al. 1953		
		Barbados	M	Alam 1979		
			M	Lucchini & Almeida 1980; Patel & Habib 1982, 1984, 1986; Silveira et al. 1987; Valicente 1989; Silva et al. 1997		
		Brazil	M	Parker et al. 1953; Guimarães 1977; Milward et al. 1991a,b,c,d,e		
			(N/G)	Etcheverry 1957		
		Chile	M	Curran 1927		
		Mexico	SC	Van Dine 1913		
		Puerto Rico	SC	Jones 1913		
		Suriname	SC,M	Segeren & Sharma 1979		
		Trinidad	M,PN	Hynes 1942		
		US	M,PN	Vickery 1929		
		<i>Archytas marmoratus</i> (Townsend)	L	Uruguay	(N/G)	Luginbill 1928
					(N/G)	Parker et al. 1953; Silveira & Ruffinelli 1956
M	Valicente & Barreto 1999; Virla et al. 1999					
Argentina	SY			Molinari & Avalos 1997		
	(N/G)			Avalos 1988		
Barbados	M			Alam 1979		
	M			Valicente 1989		
Brazil	(N/G)			Guimarães 1977		
	(N/G)			Valencia & Valdivia 1973		
Chile	(N/G)			Bruner et al. 1975		
Cuba	(N/G)			Benzing et al. 2000		
Ecuador	Ve			Malausa 1981, 1983		
Guadeloupe	M			Canas & O'Neil 1998		
Honduras	M			Cave 1993		
	P,S,M			Fennah 1947		
Lesser Antilles	M	Pair et al. 1986				
Mexico	M,S	Huis 1981; Maes 1989; Lacayo 1977				
Nicaragua	M	Sarmiento & Razuri 1978				
Peru	M	Pantoja et al. 1985; Pantoja & Fuxa 1992				
Puerto Rico	R	Van Dither 1960				
Suriname	N/G)	Yaseen 1979				
Trinidad	M	Soteres et al. 1984				
US	A					

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Archytas marmoratus</i> (Townsend)	L	Venezuela	(M	Campos 1965; Enkerlin 1975; Hogg et al. 1982; Gross & Pair 1986, 1991; Riggin et al. 1992, 1993
			M,C	Tingle et al. 1994
			M,S	Rohlf's & Mack 1985; Pair et al. 1986; McCutcheon 1991
			C,A,M,S	Butler 1958a
			M,BG,Mi	Reed 1980
			(N/G)	Ravlin & Stehr 1984
			M	Notz 1972; Fernández & Clavijo 1984
			(N/G)	Terán 1974
			M	Virla et al. 1999
			(N/G)	Guimarães 1977
<i>Archytas plangens</i> Curran	L	Argentina	M	King & Saunders 1984
		Brazil	(N/G)	Cave 1993
		Honduras	M	Estrada 1960
		Nicaragua	M	Hynes 1942
<i>Archytas</i> sp.	L	Argentina	M	Vera et al. 1995
		Brazil	SY	Molinari & Avalos 1997
		Chile	(N/G)	Guimarães 1977
		Honduras	PN	Enkerlin 1975
		Mexico	M	Wheeler et al. 1989
		Nicaragua	M	Carrillo 1980
		US	M	Estrada 1960
		US	PN	Nickle 1976
<i>Chetogena</i> sp.	L	Honduras	M	Cave 1993
<i>Cuphocerini</i> sp.	L	Argentina	(N/G)	Parker et al. 1953
<i>Eucelatoria armigera</i> (Coquillett)	L	Cuba	(N/G)	Bruner et al. 1975
		US	PN	Wall & Berberet 1975; Nickle 1976
		Venezuela	(N/G)	Terán 1974
<i>Eucelatoria australis</i> (Townsend)	L	Peru	(N/G)	Enkerlin 1975
<i>Eucelatoria bryani</i> Sabrosky	L	Honduras	S	Cave 1993
		Nicaragua	M	Maes 1989
		US	S,PN	Sabrosky 1981
<i>Eucelatoria guimaraesi</i>	L	Brazil	S,PN	Sabrosky 1981
<i>Eucelatoria rubentis</i> (Coquillett)	L	US	M	Ashley et al. 1980
			M,C	Tingle et al. 1994
			S,PN	Sabrosky 1981

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Eucelatoria</i> sp.	L	Barbados	M	Alam 1979
		Brazil	M	Silveira et al. 1987; Valicente 1989
			(N/G)	Guimaraes 1977
		Chile	PN	Enkerlin 1975
		Nicaragua	M	Maes 1989; Gladstone 1991
<i>Euphorocera floridensis</i> Townsend	L	Venezuela	M	Fernández & Clavijo 1984
			(N/G)	Terán 1974
		Honduras	(N/G)	Cave 1993
		US	PN	Wall & Berberet 1975
<i>Euphorocera tachinomoides</i> (Townsend)	L	US	PN	Wall & Berberet 1975
Syn: <i>Chetogena tachinomoides</i>				
<i>Euphorocera</i> sp.	L	Brazil	M	Goncalves & Goncalves 1973; Silva et al. 1997
			(N/G)	Guimaraes 1977
		US	(N/G)	Nickle 1976
<i>Exorista mella</i> (Walker)	L	US	PN	Wall & Berberet 1975
<i>Gonia capitata</i> DeGeer	L	US	(N/G)	Luginbill 1928
<i>Gonia crassicornis</i> (Fabricius)	L	Brazil	(N/G)	Goncalves & Goncalves 1973; Guimaraes 1977
		Honduras	S	Cave 1993
		Lesser Antilles	M	Fennah 1947
		Puerto Rico	SC	Van Dine 1913
			SC,M	Jones 1913
		US	(N/G)	Luginbill 1928
		Venezuela	(N/G)	Terán 1974
<i>Gonia (Reaumuria) pacifica</i> Townsend	L	Brazil	(N/G)	Guimaraes 1977
		Peru	(N/G)	Enkerlin 1975
<i>Gonia texensis</i> Reinhard	L	Cuba	(N/G)	Bruner et al. 1975
<i>Gonia</i> sp.	L	Chile	(N/G)	Enkerlin 1975
		Nicaragua	(N/G)	Maes 1989
<i>Hyphantrophaga hyphantriae</i> (Townsend)	L	US	(N/G)	Luginbill 1928
Syn: <i>Exorista ceratoniae</i> (Coquillett)				
<i>Hyphantrophaga collina</i> (Reinhard) Syn: <i>Zenillia blanda</i>	L	Cuba	(N/G)	Bruner et al. 1975
<i>Incamiya chilensis</i> (Aldrich)	L	Argentina	(N/G)	Blanchard 1963
		Brazil	(N/G)	Guimaraes 1977
		Chile	M	Etcheverry 1957
			(N/G)	Enkerlin 1975
		Uruguay	(N/G)	Parker et al. 1953; Silveira & Ruffinelli 1956
<i>Lespesia affinis</i> (Townsend)	L	Brazil	M	Guimaraes 1983; Silva et al. 1997

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Lespesia aletiae</i> (Riley)	L	Honduras	(N/G)	Cave 1993
		US	PN M,S M,BG,Mi	Wall & Berberet 1975 Pair et al. 1986 Reed 1980
<i>Lespesia archippivora</i> (Riley) Syn: <i>Achaetoneura archippivora</i> (Wile) Syn: <i>Frontina archippivora</i> (Scudder)	L	Argentina	M	Virla et al. 1999
		Brazil	M	Patel & Habib 1984, 1986; Guimarães 1983; Valicente 1989
			(N/G)	Guimarães 1977
		Chile	M	Etcheverry 1957
		Cuba	(N/G)	Parker et al. 1953; Ryder & Piedra 1968; Bruner et al. 1975
		Guadeloupe	M	Malausa 1981, 1983
		Guatemala	M,Te	Painter 1955
		Honduras	M	Canas & O'Neil 1998
			M,S	Cave 1993
		Lesser Antilles	M	Fennah 1947
		Mexico	M	Carrillo 1980
		Nicaragua	M	Estrada 1960; Huis 1981; Maes 1989; Gladstone 1991; Lacayo 1977
		Puerto Rico	SC	Van Dine 1913
			SC,M	Jones 1913
		US	A	Soteres et al. 1984
			C	Tingle et al. 1994
			M	Gross & Pair 1986; Riggin et al. 1992, 1993
	PN	Wall & Berberet 1975; Nickle 1976		
	PN, M	Vickery 1929		
	M,S	Pair et al. 1986		
	C,A,M,S	Butler 1958a		
	M,BG,Mi,S	Reed 1980		
	(N/G)	Luginbill 1928		
	M	Silveira & Ruffinelli 1956		
		Notz 1972; Fernández & Clavijo 1984		
		Terán 1974, 1977		
<i>Lespesia frenchi</i> (Williston)	L	Venezuela	(N/G)	Luginbill 1928
<i>Lespesia grioti</i> (Blanchard)	L	US	(N/G)	Luginbill 1928
		Argentina	M	Virla et al. 1999
			(N/G)	Blanchard 1963
		Brazil	(N/G)	Guimarães 1977

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference		
<i>Lespesia</i> sp.	L	Argentina	M (N/G)	Virla et al. 1999 Parker et al. 1953		
		Brazil	M (N/G)	Lucchini & Almeida 1980 Goncalves & Goncalves 1973; Guimarães 1977		
		Colombia	R	Vargas & Sanchez 1983		
		Cuba	(N/G)	Ryder & Pulgar 1969		
		Honduras	M	Wheeler et al. 1989		
		Nicaragua	M	Maes 1989		
		Puerto Rico	R	Pantoja et al. 1985; Pantoja & Fuxa 1992		
		US	M M,S	Ashley et al. 1980 McCutcheon 1991		
		Uruguay	(N/G)	Parker et al. 1953		
		Venezuela	M (N/G)	Notz 1972 Terán 1974		
		<i>Linnaemya annalis</i> (Townsend)	L	Venezuela	M	Terán 1977
		<i>Linnaemya comta</i> (Fallen)	L	Honduras	(N/G)	Cave 1993
		<i>Linnaemya</i> sp.	L	Ecuador	M	Benzing et al. 2000
		<i>Nemorilla pyste</i> (Walker) Syn: <i>Exorista pyste</i> (Walker)	L	US	A C (N/G)	Soteres et al. 1984 Wilson 1923 Luginbill 1928
<i>Parasetigena</i> sp.	L	Brazil	(N/G)	Guimarães 1977		
		Uruguay	(N/G)	Parker et al. 1953; Silveira & Ruffinelli 1956		
<i>Patelloa similis</i> (Townsend)	L	Brazil	M (N/G)	Patel & Habib 1984, 1986 Guimarães 1977		
		Argentina	M (N/G)	Virla et al. 1999 Parker et al. 1953		
<i>Patelloa</i> sp.	L	Uruguay	(N/G)	Parker et al. 1953; Silveira & Ruffinelli 1956		
		Chile	(N/G)	Etcheverry 1957		
<i>Peleteria robusta</i> Wiedeman	L	Chile	(N/G)	Etcheverry 1957		
<i>Phorocera claripennis</i> (Macquart) Syn: <i>Chetogena claripennis</i> (Macquart)	L	US	A (N/G)	Soteres et al. 1984 Luginbill 1928		
		Venezuela	(N/G)	Terán 1974		
		Brazil	M	Valicente 1989		
<i>Phorocera floridensis</i> (Townsend) Syn: <i>Chetogena floridensis</i> (Townsend)	L	Honduras	(N/G)	Cave 1993		
		Nicaragua	(N/G)	Maes 1989		
		US	PN	Enkerlin 1975		
			(N/G)	Luginbill 1928		
		Venezuela	(N/G)	Terán 1974		

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Pronemorilla mima</i> Townsend	L	Venezuela	M (N/G)	Notz 1972 Terán 1974
<i>Pseudokea</i> sp.	L	Brazil Chile	(N/G) M	Costa-Lima 1949 Etcheverry 1957
<i>Voria ruralis</i> (Fallen)	L	Argentina Brazil US Uruguay	M SY (N/G) M (N/G) C,A,M,S M	Virla et al. 1999 Molinari & Avalos 1997 Parker et al. 1953 Guimarães 1971 Guimarães 1977 Butler 1958a Silveira & Ruffinelli 1956
<i>Winthemia leucanae</i> (Kirkpatrick) Syn: <i>Nemorea leucanae</i> (Kirkpatrick)	L	US	M,S,BG,SY,C	Dew 1913
<i>Winthemia mima</i> (Reinhard)	L	Argentina Brazil	M (N/G)	Virla et al. 1999 Guimarães 1977
<i>Winthemia quadripustulata</i> Fabricius	L	Chile US Venezuela	M (N/G) (N/G)	Etcheverry 1957 Walton 1913; Luginbill 1928 Terán 1974
<i>Winthemia reliqua</i>	L	Chile	(N/G)	Valencia & Valdivia 1973
<i>Winthemia roblesi</i>	L	Chile	(N/G)	Valencia & Valdivia 1973
<i>Winthemia rufopicta</i> (Bigot)	L	US	A C M PN M,S PN,BG C,A,M,S M,BG,Mi,S	Soteres et al. 1984 Tingle et al. 1994 Hofmaster & Greenwood 1949; Ashley et al. 1980; Riggan et al. 1992, 1993 Wall & Berberet 1975 Rohlf's & Mack 1985; Pair et al. 1986 Enkerlin 1975 Danks 1975 Reed 1980
<i>Winthemia sinuata</i> (Reinhard)	L	US	PN	Wall & Berberet 1975
<i>Winthemia trinitatis</i> (Thompson)	L	Argentina Brazil	M M (N/G)	Virla et al. 1999 Valicente 1989 Guimarães 1977
<i>Winthemia</i> sp.	L	Argentina Brazil	M M (N/G)	Vera et al. 1995; Virla et al. 1999 Escalante 1974; Patel & Habib 1984, 1986; Silva et al. 1997 Guimaraes 1977

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Winthemia</i> sp.	L	Chile	M	Etcheverry 1957; Campos 1965
			M,PN	Enkerlin 1975
		Colombia	R	Vargas & Sánchez 1983
			M,S	Cave 1993
		Honduras	(N/G)	Fennah 1974
			M	Guevara et al. 1979
		Lesser Antilles	M	Sarmiento & Razuri 1978
			(N/G)	Yaseen 1979; Hynes 1942
		Mexico	PN	Wall & Berberet 1975
			M,S	McCutcheon 1991
Peru	(N/G)	Terán 1974		
	Venezuela			
Hymenoptera: Bethyridae				
<i>Perisierola</i> sp.	L	US	M	Bianchi 1944
Hymenoptera: Braconidae				
<i>Agathis stigmatera</i> (Cresson)	E	Argentina	M	De Santis 1967; De Santis & Esquivel 1966; Virla et al. 1999
			(N/G)	Parker et al. 1953
<i>Aleiodes caphimal</i>	L	Nicaragua	(N/G)	Andrews 1988
Syn: <i>Rogas caphimal</i>				
<i>Aleiodes laphygmae</i> (Viereck)	L	Brazil	M	Cruz et al. 1997b
Syn: <i>Rogas laphygmae</i> (Viereck)		Chile	A,M,C	Etcheverry 1957
		Honduras	M	Wheeler et al. 1989; Canas & O'Neil 1998
			M,S	Cave 1993
		Mexico	M	Molina-Ochoa et al. 2001
			M,S	Pair et al. 1986
		Nicaragua	M	Estrada 1960; Huis 1981; Maes 1989; Gladstone 1991
		Puerto Rico	R	Pantoja & Fuxa 1992
		US	M	Vickery 1929; Bianchi 1944; Ashley et al. 1982; Mitchell et al. 1984; Gross & Pair 1986; Riggan et al. 1992, 1993
			S	Rohlf's & Mack 1985
			M,S	Reed 1980; Pair et al. 1986; Isenhour 1988; McCutcheon 1991
			M,BG,PG	Ashley et al. 1983
			(N/G)	Luginbill 1928; Muesebeck et al. 1951
<i>Aleiodes terminalis</i> (Cresson)	L	Canada	A,M,C	Muesebeck et al. 1951
Syn: <i>Rogas terminalis</i> (Cresson)		US	A,M,C	Muesebeck et al. 1951
			(N/G)	Luginbill 1928; Marsh & Shaw 2001

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Aleiodes vaughani</i> (Muesebeck) Syn: <i>Rogas vaughani</i> Muesebeck	L	Honduras	M	Cave 1993; Passoa 1983; Wheeler et al. 1989; Canas & O'Neil 1998
		Nicaragua	M	Huis 1981; Maes 1989
<i>Aleiodes</i> sp. Syn: <i>Rogas</i> sp.	L	Argentina	M	Virla et al. 1999
		Cuba	M	Ryder & Pulgar 1969; Ryder & Piedra 1968
		Honduras	M	Passoa 1983
		Nicaragua	M	Estrada 1960; Maes 1989; Lacayo 1977
		US	A	Soteres et al. 1984
<i>Bassus</i> sp.	L	Argentina	(N/G)	Parker et al 1953
		Honduras	(N/G)	Cave 1993
<i>Bracon kirkpatricki</i> Wilkinson	L	Mexico	(N/G)	Moya 1980; Pena 1980
<i>Cardiochiles nigriceps</i> (Viereck)	L	US	C	Tingle et a. 1994
<i>Chelonus antillarum</i> (Marshall)	E	Barbados	M	Alam 1979
		Nicaragua	M	Ryder & Pulgar 1969
<i>Chelonus cautus</i> Cresson Syn: <i>Microchelonus cautus</i> (Cresson)	E	Honduras	M	Cave 1993; Canas & O'Neil 1998
		Mexico	M,S	Molina-Ochoa et al. 2001
		Nicaragua	M	Huis 1981
<i>Chelonus formosanus</i> (Sonan)	E	Barbados	(N/G)	Alam 1979
		Trinidad	M	Yaseen 1979
<i>Chelonus insularis</i> (Cresson) Syn: <i>Chelonus texanus</i> (Cresson)	E	Argentina	M	Virla et al. 1999
		Barbados	(N/G)	Parker et al. 1953
		Brazil	(N/G)	Alam 1979
			M	Patel & Habib 1982, 1984, 1986; Valicente 1989; Rezende et al. 1995a,b; Cruz et al. 1997a,b; Silva et al. 1997
			M,C	Rezende et al. 1994
		Chile	A,M,C	Etcheverry 1957
		Colombia	M	Medina et al. 1988
			R	Vargas & Sánchez 1983
		Cuba	BG	Myers 1932
			M	Ryder & Pulgar 1969
			(N/G)	Ryder & Piedra 1968; Bruner et al. 1975;
		Haiti	BG	Myers 1932
		Honduras	M	Wheeler et al. 1989; Canas & O'Neil 1998
			M,S	Castro et al. 1989; Cave 1993
		Lesser Antilles	M	Fennah 1947

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference		
<i>Chelonus insularis</i> (Cresson) Syn: <i>Chelonus texanus</i> (Cresson)	E	Mexico	M	Bahena & García 1991; Nava & Castro 1991; Arce & Garcia 1995; Molina-Ochoa et al. 2001		
			M, S	Pair et al. 1986		
			M	Estrada 1960; Huis 1981; Ashley 1986; Maes 1989; Gladstone 1991		
		Nicaragua	M, S	Lacayo 1977		
			R	Pantoja & Fuxa 1992		
		Puerto Rico	M	Yaseen 1979		
			(N/G)	Yaseen et al. 1981		
		Trinidad	A	Soteres et al. 1984		
			C	Tingle et al. 1994		
			M	Pierce & Holloway 1912; Vickery 1929; Bianchi 1944; Muesebeck et al. 1951; Ashley et al. 1980, 1982; Ashley 1983, 1986; Mitchell et al. 1984; Gross & Pair 1986; Riggan et al. 1992		
		US	PN	Wall & Berberet 1975		
			M, BG	Ashley et al. 1983		
			M, PN	Enkerlin 1975		
		<i>Chelonus sp.</i>	E	Uruguay	M, S	Waddill & Whitcomb 1982; Rohlf & Mack 1985; Pair et al. 1986; McCutcheon 1991
					C, A, M, S	Butler 1958b
(N/G)	Luginbill 1928					
Venezuela	(N/G)			Parker et al. 1953; Silveira & Ruffinelli 1956		
	M			Notz 1972; Fernández & Clavijo 1984		
Brazil	M			Valicente 1989		
	M			Loya-Ramírez 1978; Coronado & Ruíz 1991; Cortez & Trujillo 1994; Sánchez-García et al. 1998; Carrillo 1980		
Mexico	M, S			Molina-Ochoa et al. 2001		
	C			Herrera-Aranguena 1998		
Peru	(N/G)			Cave 1993		
	M			Maes 1989		
<i>Cotesia (Apanteles) congregata</i> (Say)	E, L ³			Honduras	M	Alam 1979
				Nicaragua	M	Wheeler et al. 1989; Virla et al. 1999
<i>Cotesia (Apanteles) glomeratus</i> (Linnaeus)	E, L ³			Barbados	M	Lucchini & Almeida 1980; Patel & Habib 1982, 1984, 1986; Cruz et al. 1997b
				Argentina	M	Etcheverry 1957
<i>Cotesia (Apanteles) marginiventris</i> (Cresson)	E, L ³	Brazil	M	Cave 1993		
		Chile	A, M, C	Fennah 1947		
Syn: <i>Apanteles grenadensis</i> (Ashmead)	E, L ³	Honduras	M			
		Lesser Antilles	M, S			

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Cotesia (Apanteles) marginiventris</i> (Cresson) Syn: <i>Apanteles grenadensis</i> (Ashmead) Syn: <i>Protapanteles harnedi</i> (Viereck) Syn: <i>Apanteles laphygmae</i> (Ashmead)	E,L ³	Mexico	M	Marsh 1978
			M,S	Pair et al. 1986; Molina-Ochoa et al. 2001
			M	Estrada 1960; Huis 1981; Maes 1989; Gladstone 1991
		Nicaragua	R	Pantoja & Fuxa 1992
			Puerto Rico	Segeren & Sharma 1979
			Suriname	(N/G) Van Dither 1960
		US	A	Soteres et al. 1984
			C	Tingle et al. 1994
			M	Muesebeck 1921; Vickery 1929; Bianchi 1944; Hofmaster & Greenwood 1949; Muesebeck et al. 1951; Marsh 1978; Ashley et al. 1980, 1982; Hogg et al. 1982; Ashley 1983, 1986; Mitchell et al. 1984; Gross & Pair 1986; Riggins et al. 1992, 1993, 1994; Hamm et al. 1994; Ruberson & Whitfield 1996
			M,S	Rohlf & Mack 1985; Pair et al. 1986; McCutcheon 1991
			PN	Wall & Berberet 1975; Nickle 1976
			M,BG	Ashley et al. 1983
		Uruguay	M,S,C,Mi	Reed 1980
(N/G)	Luginbill 1928			
(N/G)	Parker et al. 1953; Silveira & Ruffinelli 1956			
Venezuela	M	Notz 1972; Fernández & Clavijo 1984		
	SY,To	Terán 1980		
<i>Cotesia (Apanteles) ruficrus</i> (Haliday) Syn: <i>Microplitis manillee</i> (Ashmead)	E,L ³	Trinidad & Tobago	M	Yaseen 1979*
		US	(N/G)	McCutcheon et al. 1983**; Rajapakse et al. 1985***
<i>Cotesia (Apanteles) sp.</i>	E,L ³	Barbados	M	Alam 1979
			Brazil	M
		Colombia	R	Vargas & Sánchez 1983
			M	Medina et al. 1988
		Guyana	M	Sinha 1982
			Nicaragua	M
		Peru	M,S	Lacayo 1977
			C	Herrera-Aranguena 1998
			Trinidad	M
		US	M	Hofmaster & Greenwood 1949
M	Cave 1993			
<i>Distatrix sp.</i>	L	Honduras	M	Cave 1993
		Honduras	M	Cave 1993
<i>Glyptapanteles militaris</i> (Walsh)	L	US	S	Rohlf & Mack 1985
			(N/G)	Muesebeck et al. 1951

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Gnathopleura</i> sp.	L	Honduras	(N/G)	Cave 1993
<i>Homolobus truncator</i> (Say)	L	Honduras	M,S	Cave 1993
Syn: <i>Zele mellea</i> (Cresson)		Nicaragua	M	Huis 1981; Maes 1989
		US	A	Soteres et al. 1984
			M	Vickery 1929; Wall & Berberet 1975; Riggin et al. 1992, 1993
			M,S	Pair et al. 1986; McCutcheon 1991
			M,S,C	Reed 1980
			(N/G)	Luginbill 1928
<i>Macrocentrus</i> sp.	L	Barbados	(N/G)	Alam 1979
		Brazil	M	Silva et al. 1997
<i>Meteorus arizonensis</i> (Muesebeck)	L	Honduras	(N/G)	Cave 1993
		Nicaragua	M	Maes 1989
<i>Meteorus autographae</i> (Muesebeck)	L	Mexico	M,S	Pair et al. 1986
		US	A	Soteres et al. 1984
			C	Tingle et al. 1994
			M	Ashley et al. 1980, 1982; Mitchell et al. 1984; Gross & Pair 1986; Riggin et al. 1992, 1993
			PN	Nickle 1976
			S	Rohlf's & Mack 1985
			M,S	Pair et al. 1986; McCutcheon 1991
			M,BG,Mi	Reed 1980
			M,BG,PG	Ashley et al. 1983
			(N/G)	Luginbill 1928; Muesebeck et al. 1951
<i>Meteorus laphygmae</i> (Viereck)	L	Chile	M	Etcheverry 1957
		Colombia	M	Medina et al. 1988
			R	Vargas & Sánchez 1983
			C,S	Ortegón et al. 1988
		Honduras	M,S	Cave 1993
		Mexico	M	Molina-Ochoa et al. 2001
			S	Ciceros et al. 1995
		Nicaragua	(N/G)	Gladstone 1991
		Suriname	M,PN	Segeren & Sharma 1979
			(N/G)	Van Dither 1960
		US	M	Vickery 1929; Bianchi 1944
			M,BG	Enkerlin 1975
			(N/G)	Luginbill 1928

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Meteorus laphygmae</i> (Viereck)	L	Venezuela	M	Notz 1972; Terán 1980; Fernández & Clavijo 1984; Fernández & Terán 1990a,b
<i>Meteorus vulgaris</i> (Cresson)	L	US	(N/G)	Luginbill 1928; Muesebeck et al. 1951
<i>Meteorus</i> sp.	L	Mexico	M	Peraza-Lizarraga 1982; Coronado & Ruiz 1991
		Peru	M, S	Molina-Ochoa et al. 2001
			C	Herrera-Aranguena 1998
<i>Microplitis</i> sp.	L	Uruguay	(N/G)	Parker et al. 1953; Silveira & Ruffinelli 1956
<i>Palinzele</i> sp.	L	Trinidad	M	Yaseen 1979
<i>Stantonia</i> sp.	L	Honduras	(N/G)	Cave 1993
		Nicaragua	M	Maes 1989
Hymenoptera: Chalcididae				
<i>Brachymeria ovata</i> (Say)	P	Argentina	M	Virla et al. 1999
		US	(N/G)	Parker et al. 1953
			M	Ashley 1979
<i>Brachymeria robusta</i> (Cresson)	P	US	C	Wilson 1923
			(N/G)	Luginbill 1928
<i>Conura (Spilochalcis) femorata</i> (Fabricius)	L	Honduras	(N/G)	Cave 1993
		Nicaragua	(N/G)	Maes 1989
		US	C	Wilson 1923
			(N/G)	Luginbill 1928
<i>Conura (Ceratosmicra) hirtifemora</i> (Ashmead)	L	US	M	Riggin et al. 1992, 1993
Syn: <i>Splilochalcis hirtifemora</i> (Ashmead)				
<i>Conura (Ceratosmicra) immaculata</i> (Cresson)	L	Honduras	(N/G)	Cave 1993
Syn: <i>Conura fulvomaculata</i> (Cameron)		Nicaragua	M	Maes 1989
<i>Conura (Ceratosmicra) meteori</i> (Burks)	L	US	M	Hofmaster & Greenwood 1949
<i>Conura igneoides</i> (Kirby)	L	US	C	Wilson 1923
Syn: <i>Splilochalcis vittata</i> (Ashmead)			(N/G)	Luginbill 1928; Muesebeck et al. 1951
Hymenoptera: Eulophidae				
<i>Euplectrus comstockii</i> Howard	L	Nicaragua	M	Maes 1989
		US	(N/G)	Luginbill 1928
<i>Euplectrus furnicus</i> Walker	L	Argentina	M	De Santis 1979; De Santis 1989; De Santis & Fidalgo 1994; Virla et al. 1999
		Puerto Rico	R	Pantoja & Fuxa 1992
<i>Euplectrus hircinus</i> (Say)	L	Panama	(N/G)	Andrews 1988
<i>Euplectrus insularis</i> Howard	L	Honduras	M	Wheeler et al. 1989
		Nicaragua	(N/G)	Huis 1981

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Euplectrus marginatus</i> Ashmead	L	Nicaragua	M	Maes 1989
<i>Euplectrus plathypenae</i> Howard	L	Barbados	M	Alam 1979
		Brazil	(N/G)	Costa-Lima 1962
		Chile	M	Etcheverry 1957
		Colombia	M	Vargas & Sánchez 1983
		Cuba	Pm&Pb	Myers 1932
			(N/G)	Ryder & Piedra 1968; Bruner et al. 1975
		Guyana	M	Sinha 1982
		Lesser Antilles	M	Fennah 1947
		Mexico	M	Guevara et al. 1979; Montoya-Burgos 1980; Gutiérrez-Rodríguez 1982; Molina-Ochoa et al. 2001
		Nicaragua	M	Ryder & Pulgar 1969
		Puerto Rico	R	Pantoja & Fuxa 1992
		Trinidad	(N/G)	Yaseen 1979
		US	M	Vickery 1929; Muesebeck et al. 1951; Ashley et al. 1980, 1982; Hogg et al. 1982; Riggin et al. 1992, 1993
			PN	Wall & Berberet 1974, 1975
			(N/G)	Luginbill 1928
		Venezuela	M	Marín-Acosta 1966
			S,C	Guagliami 1962
<i>Euplectrus ronnai</i> (Brethes)	L	Brazil	M	De Santis 1980
<i>Euplectrus</i> sp.	L	Brazil	M	Lucchini & Almeida 1980
		Cuba	BG	Myers 1932
		Honduras	M	Cave 1993
		Mexico	M	Montoya-Burgos 1979, 1980; Cortez & Trujillo 1994
			M,S	Pair et al. 1986
		Nicaragua	M	Huis 1981
			M,S	Lacayo 1977
		US	BG	Reed 1980
			M	Keller 1980
			M,S	Pair et al. 1986
			(N/G)	Enkerlin 1975
<i>Trichodischia caerulea</i>	L	Brazil	(N/G)	Guimaraes 1977
<i>Trichodischia soror</i> (Bigot)	L	Argentina	M	Virla et al. 1999
			(N/G)	Parker et al. 1953; Blanchard 1963
		Brazil	(N/G)	Cortes 1980
<i>Trichospilus pupivora</i> (Ferriere)	P	Barbados	M	Alam 1979
<i>Trichospilus</i> sp.	L	Argentina	(N/G)	Parker et al. 1953

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
Hymenoptera: Ichneumonidae				
<i>Amblyteles</i> sp.	L	Brazil	(N/G)	Costa-Lima 1949
		Chile	M	Etcheverry 1957
<i>Ancyloneura</i> sp.	L	Argentina	(N/G)	Parker et al. 1953
<i>Anomalon ejuncidum</i> (Say)	L	US	M,S	Pair et al. 1986
<i>Campoletis chloridae</i> (Vierech)	L	Barbados	M	Alam 1979
<i>Campoletis curvicauda</i> (Blanchard)	L	Peru	M	Ayqui-Vilca 1993
<i>Campoletis flavicincta</i> (Ashmead)	L	Brazil	M	Patel & Habib 1982, 1984, 1986; Cruz et al. 1997a,b
		Honduras	(N/G)	Cave 1993
		Mexico	M,S	Molina-Ochoa et al. 2001
		Nicaragua	M	Huis 1981; Maes 1989
		US	A	Soteres et al. 1984
			M	Hogg et al. 1982
			PN	Wall & Berberet 1975
		Uruguay	(N/G)	Parker et al. 1953; Yaseen et al. 1981
<i>Campoletis grioti</i> (Blanchard)	L	Argentina	M	Virla et al. 1999
		Brazil	M	Lucchini & Almeida 1980; Silveira et al. 1987; Cruz et al. 1997b
		US	M	Ashley 1983
		Uruguay	M	Morey 1971
<i>Campoletis oxylus</i> (Cresson)	L	US	M	Muesebeck et al. 1951
Syn: <i>Sagaritis oxylus</i> (Cresson)			M,S	Pair et al. 1986
			(N/G)	Luginbill 1928
<i>Campoletis sonorensis</i> (Cresson)	L	Brazil	M	Cruz et al. 1997b
		Chile	M	Machuca et al. 1989
		Honduras	M	Canas & O'Neil 1998
			M,S	Cave 1993
		Mexico	M,S	Pair et al. 1986
		US	A	Soteres et al. 1984
			M	Gross & Pair 1986; Riggin et al. 1992, 1993
			M,S	Pair et al. 1986; Isenhour 1988
<i>Campoletis</i> sp.	L	Argentina	M	Vera et al. 1995
		Brazil	M	Silva et al. 1997; Silveira et al. 1987; Valicente & Barreto 1999
			(N/G)	Cruz et al. 1999
		Nicaragua	M	Maes 1989
		US	M,S	McCutcheon 1991

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Campoplex</i> sp.	L	Brazil	M	Silva et al. 1997
<i>Cryptus albitarsis</i> (Cresson)	P	US	M	Pair & Gross 1989
<i>Diadegma</i> sp.	L	Argentina	M	Porter 1998; Virla et al. 1999
		Brazil	M	Silva et al. 1997
		Cuba	M	Ayala-Sifontes et al. 1978
		Mexico	M	Flores-Dávila et al. 1991
<i>Diapetimorpha introita</i> (Cresson)	P	Honduras	M	Cave 1993
		US	M	Pair & Gross 1984, 1989
			M,S	Pair et al. 1986
<i>Eiphosoma annulatum</i> (Cresson)	L	Venezuela	M	Notz 1972
<i>Eiphosoma vitticole</i> (Cresson)	L	Bolivia	M	Ashley 1979
			(N/G)	Yaseen et al. 1981
		Brazil	M	Patel & Habib 1982, 1984, 1986; Valicente 1989; Silveira et al. 1987; Cruz et al. 1997b
		Colombia	M	Medina et al. 1988
		Honduras	M	Wheeler et al. 1989; Canas & O'Neil 1998
			M,S	Cave 1993
		Mexico	M,S	Pair et al. 1986
		Nicaragua	M	Huis 1981
		US	M	Ashley 1983
		Venezuela	(N/G)	Giraldo-Vanegas & Garcia-R. 1992, 1994a,b, 1995
<i>Eiphosoma</i> sp.	L	Brazil	M	Cruz et al. 1997a; Silva et al. 1997
		Mexico	M	Cortez & Trujillo 1994
		Trinidad	M	Hynes 1942
			(N/G)	Yaseen et al. 1981
		Venezuela	M	Fernández & Clavijo 1984
<i>Enicospilus flavus</i> (Fabricius)	L	US	C	Wilson 1923
Syn: <i>Enicospilus concolor</i> (Cresson)			(N/G)	Luginbill 1928
<i>Enicospilus merdarius</i> (Gravenhorst)	L	Argentina	M	Muesebeck et al. 1951
Syn: <i>Enicospilus purgatus</i> (Say)		Cuba	M	Bruner et al. 1975
		Honduras	(N/G)	Cave 1993
		Nicaragua	M	Maes 1989
		US	C,M	Dew 1913
			(N/G)	Luginbill 1928
<i>Goryphina</i> sp.	L	Brazil	M	Silva et al. 1997
<i>Hyposoter</i> sp.	L	Honduras	M	Cave 1993
		Uruguay	(N/G)	Parker et al. 1953; Silveira & Ruffinelli 1956

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Ichneumon ambulatorius</i> Fabricius	P	US	M	New record (JEC)
<i>Ichneumon promissorius</i> (Cresson)	P	US	M	New record (JEC)
<i>Isdromas lycanae</i> (Howard)	L	US	M	Riggin et al. 1992, 1993
<i>Mesochorus disceitergus</i> (Say)	L	US	M	Hofmaster & Greenwood 1949; Riggin et al. 1992, 1993
<i>Microcharops anticarsiae</i> (Gupta)	L	Honduras	M S	Wheeler et al. 1989 Cave 1993
<i>Netelia sayi</i> (Cushman)	L	US	C	Tingle et al. 1994
<i>Netelia</i> sp.	L	Peru	M	Escalante 1974
		US	A	Soteres et al. 1984
<i>Parania (Atrometus) tricolor</i> (Morley)	L	Uruguay	(N/G)	Parker et al. 1953; Silveira & Ruffinelli 1956
<i>Pristomerus spinator</i> (Fabricius)	L	Brazil	M	Patel & Habib 1984, 1986
Syn: <i>Neopristomerus appalachianus</i> (Viereck)		Honduras	M	Wheeler et al. 1989; Canas & O'Neil 1998
			M,S	Cave 1993
		Mexico	M	Carrillo 1980
			M,S	Pair et al. 1986; Molina-Ochoa et al. 2001
		Nicaragua	M	Estrada 1960; Huis 1981; Gladstone 1991; Maes 1989; Lacayo 1977
		US	A	Soteres et al. 1984
			C	Tingle et al. 1994
			M	Vickery 1929; Bianchi 1944
			PN	Wall & Berberet 1975
			M,S	Pair et al. 1986
			(N/G)	Luginbill 1928
<i>Ophion ancyloneura</i> (Wichsee)	L	Argentina	M	De Santis 1967; Virla et al. 1999
			(N/G)	Parker et al. 1953
		Uruguay	(N/G)	Silveira & Ruffinelli 1956
<i>Ophion bilineatus</i> (Say)	L	Chile	M	Etcheverry 1957
		US	M	Vickery 1929
			PN	Enkerlin 1975
			(N/G)	Luginbill 1928
<i>Ophion flavidus</i> (Brulle)	L	Argentina	M	Virla et al. 1999
		Brazil	M	Goncalves 1973; Patel & Habib 1982, 1984, 1986; Silveira et al. 1987
		Honduras	M	Wheeler et al. 1989; Canas & O'Neil 1998
			M,S	Cave 1993
			(N/G)	Passoa 1983

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Ophion flavidus</i> (Brulle)	L	Mexico	M	Molina-Ochoa et al. 2001
			M,S	Pair et al. 1986
		Nicargua	M	Maes 1989; Gladstone 1991
		US	M	Hogg et al. 1982; Gross & Pair 1986, 1991; Riggin et al. 1992, 1993
			M,S M,BG,Mi,S	Rohlf's & Mack 1985; Pair et al. 1986 Reed 1980
<i>Ophion merdarius</i> (Gravenhorst) Syn: <i>Enicospilus purgatus</i> (Gravenhorst)	L	Nicaragua	M	Maes 1989
		US	(N/G)	Luginbill 1928
<i>Ophion</i> sp.	L	Argentina	M	Vera et al. 1995
		Brazil	M	Silva et al. 1997
		Mexico	M	Ashley 1986
		Nicaragua	M	Huis 1981; Maes 1989
		Peru	M	Escalante 1974
		US	C	Tingle et al. 1994
			M	Mitchell et al. 1984
			PN	Nickle 1976
			M,PG	Ashley et al. 1983
			(N/G)	Parker et al. 1953
<i>Sagaritis dubitatus</i> (Cresson)	L	Uruguay	M	Vickery 1929
		US	(N/G)	Luginbill 1928
<i>Trachysphyrus cleonis</i> (Viereck)	L	Peru	M	Escalante 1974
<i>Temelucha difficilis</i> (Dasch.)	L	US	M	Mitchell et al. 1984; Gross & Pair 1986
			M,S	Pair et al. 1986
<i>Temelucha grapholithae</i> (Cushman)	L	Honduras	M	Canas & O'Neil 1998
			M,S	Cave 1993
			M	Gladstone 1991
<i>Temelucha</i> sp.	L	Honduras	M	Wheeler et al. 1989
		Nicaragua	M	Maes 1989
		US	M	Ashley et al. 1980, 1982, 1983
		US	M	Pair & Gross 1989
<i>Vulgichneumon brevicintor</i> (Say)	P	US	M	Pair & Gross 1989
Hymenoptera: Perilampidae				
<i>Perilampus hyalinus</i> (Say) (Reported as hiperparasitoid)	L	Honduras	M	Cave 1993
		Venezuela	M	Notz 1972

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
Hymenoptera: Pteromalidae				
<i>Catalaccus aeneoviridis</i> (Girault)	L	US	M	Hofmaster & Greenwood 1949
<i>Trichomalopsis viridescens</i> (Walsh) Syn: <i>Eupteromalus viridescens</i>	L	US	M	Hofmaster & Greenwood 1949; Riggin et al. 1992, 1993
Hymenoptera: Scelionidae				
<i>Telenomus remus</i> (Nixon)	E	Antigua	M	Irving 1978
		Barbados	M	Alam 1979
		Brazil	M	Correa-Figueiredo et al. 1999
		Colombia	M	Alvarez & Roa 1995
		Dominican Republic	(N/G)	Yaseen et al. 1981
		Guadeloupe	(N/G)	Yaseen et al. 1981
		Guyana	M,S	Sinha 1982
		Honduras	M	Cave & Acosta 1999
		Nicaragua	M	Maes 1989
		Puerto Rico	(N/G)	Wojcik et al. 1976
		Suriname	M	Segeren & Sharma 1979
		Trinidad	M	Yaseen 1979
		US	M,S	Waddill 1977; Waddill & Whitcomb 1982
			(N/G)	Wojcik et al. 1976
		Venezuela	M	Hernández et al. 1989; Hernandez & Díaz 1995, 1996a,b; Gonzalez-Narvaez & Zocco 1996; Ferrer 1998a,b
<i>Telenomus</i> sp.	E	Brazil	M	Cruz et al. 1999
		Colombia	M	Alvarez & Roa 1995
			R	Vargas & Sánchez 1983
		Cuba	M	Armas-García & Ayala-Sifontes 1987; Ayala-Sifontes et al. 1992
		Guadeloupe	M	Malaua 1983
		Mexico	M	Montoya-Burgos 1979; Morales-Pérez 1982; Canseco-Román 1988; García-Lagunas 1988; Barilla-Vera 1989
Hymenoptera: Trichogrammatidae				
<i>Trichogramma demoraesi</i> (Zucchi)	E	Chile	M	Pratissoli et al. 1999
<i>Trichogramma fasciatum</i> Perkins	E	Barbados	M	Alam 1979
		Nicaragua	M	Maes 1989
<i>Trichogramma minutum</i> Riley	E	Nicaragua	M	Maes 1989
		US	M	Muesebeck et al. 1951
			(N/G)	Luginbill 1928

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Trichogramma pretiosum</i> (Riley)	E	Brazil	M	De Sa & Parra 1994; Zucchi et al. 1991
		Nicaragua	M	Huis 1981
<i>Trichogramma</i> sp.	E	Argentina	M	Virla et al. 1999
		Brazil	M	De Sa & Parra 1994
			(N/G)	Cruz et al. 1999
		Colombia	R	Vargas & Sánchez 1983
		Cuba	M	Armas-García & Ayala-Sifontes 1987; Ayala-Sifontes et al. 1988
		Guadeloupe	M	Malausa 1983
			(N/G)	Yaseen et al. 1981
		Mexico	M	Loya-Ramírez 1978; Montoya-Burgos 1979, 1980; Guevara et al. 1979; Rodríguez-Luna 1982; Wong-Arevalo 1982; Johannes-Toonders & Carrillo-Sánchez 1987
			(N/G)	Bahena & García 1991
			M	Huis 1981; Maes 1989; Mulock et al. 1990
		Nicaragua	M	Waddill & Whitcomb 1982
		US	M,S	
Nematoda: Acugutturidae				
<i>Noctuidonema guyanense</i> Remillet & Silvain	A	Bahamas	(N/G)	Simmons & Rogers 1990b
		Belize	(N/G)	Simmons & Rogers 1990b
		Bermuda	(N/G)	Simmons & Rogers 1990b; Simmons et al. 1991
		Cayman Islands	(N/G)	Simmons & Rogers 1990b
		Colombia	(N/G)	Simmons & Rogers 1990b
		Costa Rica	(N/G)	Simmons & Rogers 1990b
		Dominica	(N/G)	Simmons & Rogers 1990b
		El Salvador	(N/G)	Simmons & Rogers 1990b
		French Guiana	(N/G)	Remillet & Silvain 1988; Marti et al. 1990; Rogers et al. 1990a, 1991, 1993; Silvain & Remillet 1993; Marti et al. 2000
		Grenada	(N/G)	Simmons & Rogers 1990b; Simmons et al. 1991
		Guadeloupe	(N/G)	Marti et al. 2000
		Honduras	(N/G)	Simmons & Rogers 1990b
		Martinique	(N/G)	Simmons & Rogers 1990b; Marti et al. 1990
		Mexico	(N/G)	Simmons & Rogers 1990b
		Panama	(N/G)	Simmons & Rogers 1990b; Simmons et al. 1991
		Puerto Rico	(N/G)	Simmons & Rogers 1990b; Simmons et al. 1991

TABLE 1. (CONTINUED) FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE), PARASITES AND PARASITOIDS IN THE AMERICAS AND CARIBBEAN BASIN WITH ACCOMPANYING REFERENCES INDICATING FAMILY, HOST STAGE ATTACKED, CROPS FROM WHICH FALL ARMYWORM WERE COLLECTED AND COUNTRIES OF COLLECTION.

Classification of parasite and parasitoid	Host stage attacked ¹	Country of collection	Crop ²	Reference
<i>Noctuidonema guyanense</i> Remillet & Silvain	A	Suriname	(N/G)	Simmons & Rogers 1990b
		Trinidad	(N/G)	Simmons & Rogers 1990b
		US	(N/G)	Marti et al. 1990; Simmons & Rogers 1990b; Rogers et al. 1990b, 1991, 1993, 1996; Simmons et al. 1991; Simmons & Rogers, 1990a, b, 1991, 1994; Marti et al. 2000; Rogers & Marti 1994, 1996
			M	Simmons & Marti 1992
		Virgin Island	M, S (N/G)	Rogers & Marti 1992a, b, 1993a; Marti & Rogers 2000 Simmons & Rogers 1990b

*Imported from Pakistan, ** Imported from Australia, *** Imported from Thailand & Imported from India.

¹Host stage attacked: E (Egg), L (Larva), P (Pupa), A (Adult).

²A = Alfalfa (*Medicago sativa* L.), BG = Bermudagrass (*Cynodon dactylon* L.), C = Cotton (*Gossypium* spp.), M = Maize (*Zea mays* L.), Mi = Millet (*Panicum miliaceum* L.), O = Onion (*Allium cepa* L.), P = Hot pepper (*Capsicum annuum* L.), Pb = (*Panicum barbinode* L.), PG = Paragrass (*Brachiaria mutica* L.), Pm = (*P. maximum* L.), PN = Peanut (*Arachis hypogaea* L.), R = Rice (*Oryza sativa* L.), S = Sorghum (*Sorghum bicolor* L. (Moench.)), SC = Sugarcane (*Saccharum officinarum* L.), SY = Soybean (*Glycine max* L.), T = Tomato (*Lycopersicon esculentum* L.), Te = Teosinte (*Euchlaena mexicana* Schard), To = Tobacco (*Nicotiana tabacum* L.), Ve = Vegetable Crops, (N/G) = Not given.

³Reported attacking eggs and larva (no confirmation).

TABLE 2. NUMBER OF SPECIES IN EACH TAXON REPORTED FROM DIFFERENT REGIONS.

Order	Family	Region		
		North America (Mexico-US)	Central America & Caribbean Basin	South America
Diptera				
	Bombyliidae	1		
	Phoridae		1	
	Sarcophagidae	3	3	1
	Tachinidae	29	24	38
Hymenoptera				
	Bethylidae	1		
	Braconidae	18	22	11
	Chalcididae	6	2	1
	Eulophidae	3	8	7
	Ichneumonidae	27	18	21
	Perilampidae		1	1
	Pteromalidae	2		
	Scelionidae	2	2	2
	Trichogrammatidae	2	4	3
Nematoda				
	Aphelenchoididae	1	1	1

RESULTS AND DISCUSSION

A great diversity of parasitoids and parasites of FAW has been reported occurring in the Americas and the Caribbean basin. In this inventory, approximately 150 species of parasitoids and parasites have been recorded from 14 families, nine in Hymenoptera, four in Diptera and one in Nematoda (Table 1). Ichneumonids and braconids were the most diverse families in Hymenoptera, represented by 36 and 28 species, respectively. The most diverse family in Diptera, as well as overall, was Tachinidae with 55 species.

Distribution among the taxa was highly variable. Three of the 14 families were only reported from one country, and five of the 14 families were reported from two or fewer countries. Bethyloid and bombyliid parasitoids were only reported in the United States (US) during the 1920s and 1940s (Table 1). Of the ≈ 150 species, 74 were reported from only one country, and 102 were reported from only one geographical region. In contrast, nine of the 14 families and 18 of the ≈ 150 species were reported from all geographical regions (North America, Central America and the Caribbean, and South America), and eight species were reported from 10 or more countries (Tables 1 and 2).

The number of parasitoid and parasite species reported from each FAW stage attacked in each country is summarized in Table 3. The highest number of parasitoid species attacking FAW larvae was reported from the US (75), followed by Brazil (45), Honduras (43) and Nicaragua (42).

Parasitoid species that attack FAW eggs were more prevalent in Nicaragua (11) Brazil (8), Barbados (7) and Mexico (6). Parasitoid species that attack FAW pupae were reported from only 4 countries, with the greatest number of these species collected from the US (6).

Parasitized FAW were collected from 19 different host plants (Table 4). FAW collected from corn were parasitized by species from all families except Bombyliidae. The number of parasite and parasitoid species attacking FAW was greatest for FAW collected from corn (134), sorghum (40), cotton (28), peanut (24), alfalfa (17), rice (13), and Bermuda grass (11). Six of the 14 parasitoids and parasite families were recovered from FAW that had been collected from a single host plant species. Ten of the 14 parasitoids and parasite families were recovered from FAW that had been collected from three or fewer host plant species. The most diverse parasitoid families also were recovered from more FAW host plant species. Tachinids, braconids, eulophids, and ichneumonids were recovered from FAW collected from 15, 11, 8 and 8 FAW host plant species, respectively.

A considerable number of parasitoid species ($\approx 33\%$) were reported only from one geographical region (Table 1). These findings emphasize the need for more surveys and taxonomical studies of the natural enemies in the different habitats of the natural distribution of the pest (Molina-Ochoa et al. 2001). It is important to consider the different developmental stages of the pest and the growing season of the crop to determine if differ-

TABLE 3. NUMBER OF SPECIES OF PARASITOIDS AND STAGE HOST ATTACKED REPORTED FROM DIFFERENT COUNTRIES.

Country	Number of parasitoid species			
	Egg	Larval	Pupae	Adult
Antigua	1			
Argentina	4	28	1	
Bahamas				1
Barbados	7	9	1	
Belize				1
Bermuda				1
Bolivia		1		
Brazil	8	45		
Cayman Is.				1
Canada		1		
Chile	3	19		
Colombia	5	6		1
Costa Rica				
Cuba	3	11		
Dominica				1
Dominican Republic	1			
Ecuador		2		
El Salvador				1
French Guinea				1
Grenada				1
Guadeloupe	3	2		1
Guatemala		1		
Guyana	2	2		
Haiti	1			
Honduras	5	43	1	1
Lesser Antilles	2	8		
Martinique				1
Mexico	6	22		
Nicaragua	11	42		
Panama		1		
Peru	2	10		
Puerto Rico	3	9		1
Suriname	2	4		1
Tobago	1	1		
Trinidad	4	9		1
United States	3	75	7	1
Uruguay	1	16		
Venezuela	2	29		
Virgin Is.				1

ences in natural distribution of the parasitoids exist (Ashley 1979; Molina-Ochoa et al. 2001) or if the records related to unique occurrence are due to inadequate surveys. It also is important to determine if the occurrence of FAW parasitoids is associated with the developmental stage of the pest and the host plant. Studies related to tritrophic interactions are needed to elucidate the role of the plant metabolites on the susceptibility of the pest to parasitoids and pathogens, as well as their suitability (Molina-Ochoa et al. 1999). A high diversity of FAW parasitoids has been reported in its natural distribution exerting significant mortal-

ity on egg and larval populations. An understanding of induced parasitization of the complex of parasitoids is needed to determine the species with higher capability to attack each stage of the FAW. It is necessary to unite institutional efforts to establish programs of release of FAW parasitoids in overwintering areas and to reduce the migration of the pest northward (Gross & Pair 1986). Because much of the published work does not include environmental data with the collections, we encourage authors to include this information in the future. These data would help select candidate parasitoids for a specific or broad region.

TABLE 4. NUMBER OF PARASITOID SPECIES IN EACH TAXON REPORTED FROM FAW COLLECTED FROM DIFFERENT HOST PLANTS.

Order	Family	FAW host plants																		
		A	BG	C	M	Mi	O	P	Pb	PG	Pm	PN	R	S	SC	SY	T	Te	To	Ve
Diptera																				
	Bombyliidae		1																	
	Phoridae				1															
	Sarcophagidae				4															
	Tachinidae	6	4	7	34	4	1	1				15	4	13	3	5	1	1		1
Hymenoptera																				
	Bethylidae				1															
	Braconidae	7	4	12	24	2				2		4	5	11		1				1
	Chalcididae			3	4															
	Eulophidae		1	1	9					1	1	1	2	2						
	Ichneumonidae	4	1	5	36	1				1		4		11						
	Perilampidae				1															
	Pteromalidae				2															
	Scelionidae				2							1	1							
	Trichogrammatidae				5							1	1							
Nematoda																				
	Acuguttuidae				1									1						

A = Alfalfa, BG = Bermuda grass, C = Cotton, M = Maize, Mi = Millet, O = Onion, P = Hot Pepper, Pb = *Panicum barbinode*, PG = Para grass, Pm = *P. maximum*, PN = Peanut, R = Rice, S = Sorghum, SC = Sugarcane, SY = Soybean, T = Tomato, Te = Teosinte, To = Tobacco, Ve = Vegetable crops

Parasites and Parasitoids of *Spodoptera frugiperda*
Pupae and Adults

Spodoptera frugiperda pupae and adults are attacked by several parasite and parasitoid species. Five species of Ichneumonidae: *Diapetimorpha introita* (Cresson), *Cryptus albitarsis* (Cresson), *Ichneumon promissorius* (Erichson), *Ichneumon ambulatorius* and *Vulgichneumon brevicinctor* (Say) have been reported attacking pupae of *S. frugiperda* and other noctuids (Bechinski & Pedigo 1983; Pair & Gross 1984; Wilson 1983; Pair & Gross 1989; Fitt & Daly 1990; Pavuk & Stinner 1991). Two generalist pupal parasitoids of Chalcididae, *Brachymeria ovata* (Say) and *B. robusta* (Cresson), have been collected from *S. frugiperda* (Wilson 1923; Luginbill 1928; Parker et al. 1953; Ashley 1979; Virla et al. 1999). Only one eulophid species, *Trichospilus pupivora* (Ferriere), has been reported as a generalist parasitoid of Lepidopteran pupae, including *S. frugiperda* (Alam 1979, Anantanarayanan 1934). Also, only one species (the ectoparasitic nematode, *Noctuidonema guyanense* Remillet & Silvain (Remillet & Silvain 1988)), has been observed parasitizing *S. frugiperda* adults.

Studies on *Diapetimorpha introita*

Diapetimorpha introita, a parasitoid which attacks FAW in the pupal stage, was reported for first time by Pair & Gross (1984) in Tifton, Georgia. The levels of parasitization in six trials ranged from 0.0 to 23.7%, and the percent of intact pupae that were parasitized during that study averaged 13.5%. Later, Gross & Pair (1986) emphasized the need for more efforts to explore the role of species of parasitoids that employ similar strategies. Pair & Gross (1989) reported the seasonal incidence of *D. introita* with rates of parasitism that averaged 5.2% (range 0-23.7%) and 8.4% (range 0-50.0%), respectively, during 1983 and 1984, with the highest rate occurring during September to November of each year. Because male *D. introita* are attracted to chemicals emitted by the female wasps (Jewett & Carpenter 1998) sticky traps baited with live female wasps were used to study the seasonal abundance of *D. introita* (Jewett & Carpenter 2001). The highest number of adult males was caught during early autumn which corresponded to the rates of parasitism reported by Pair and Gross (1989). As the investigation of their importance to biological control of *Spodoptera* spp. proceeds, more convenient methods of monitoring *D. introita* in the field are needed.

Pair (1995) studied the biology and rearing of *D. introita* on host and non-host noctuid pupae, *Spodoptera* spp., *Helicoverpa zea* (Boddie), and *Heliothis virescens* (F.) to identify factors that influence the reproduction and developmental rate of *D. introita*. This parasitoid was successfully

reared in the laboratory on *S. frugiperda* pupae. Carpenter & Greany (1998) compared the developmental time, weight, fecundity, longevity, and ability to parasitize hosts for *D. introita* wasps developing on artificial diet and wasps reared on *S. frugiperda* pupae. They conclude that the ability to rear *D. introita* on an inexpensive, artificial diet significantly enhances the potential of mass rearing this parasitoid for inundative releases against species in the genus *Spodoptera*.

Studies on *Ichneumon promissorius*
and Collection of *Ichneumon ambulatorius*

I. promissorius was collected in Australia from *Helicoverpa armigera* (Hübner), and *H. punctigera* (Wallengren) pupae (Chadwick & Nikitin 1976; Wilson 1983; Fitt & Daly 1990). The parasitoid was imported into the US and released in Arkansas, Georgia, Oklahoma, and Texas from 1992 to 1997 (J. E. C. et al., unpublished data). Following releases of *I. promissorius* in ear-stage corn in the lower Rio Grande valley in Texas during 1993 and 1994, feral noctuid pupae, including FAW, were removed from the soil. During 1993, 575 FAW pupae were collected, 8 of which were parasitized by *I. promissorius*. Of the 13 FAW pupae collected in 1994, none were parasitized by *I. promissorius*. A similar study was conducted in a cornfield in Rabun County, Georgia. During 1993, 141 of the 300 FAW pupae collected were parasitized by *I. promissorius* and 24 were parasitized by *I. ambulatorius*, a new host record. Only 5 FAW pupae collected in 1994. Two of these FAW pupae were parasitized by *I. promissorius* and one was parasitized by *I. ambulatorius*.

Carpenter et al. (1994) compared several indigenous lepidopteran species in Tifton, GA, for *I. promissorius* acceptance and development. Pupae of *H. zea*, *H. virescens* (F.), *H. subflexa* (Guenée), *S. frugiperda*, *S. exigua* (Hübner), *Trichoplusia ni* (Hübner), *Agrotis ipsilon* (Hufnagel), and *Anticarsia gemmatalis* (Hübner) were used as hosts. Ninety pupae/species were tested, resulting in 74, 72, 68, 66, and 62 wasps emerging from *T. ni*, *A. ipsilon*, *H. subflexa*, *S. exigua*, and *S. frugiperda*, respectively. Lowest emergence of wasps was obtained on *A. gemmatalis* (6). The most acceptable hosts of *I. promissorius* were *H. zea* and *H. virescens*, as expected because *I. promissorius* was collected in Australia from heliothid species (Fitt & Daly 1990). Carpenter et al. (1994) considered that *H. zea* should be the primary host species of this pupal parasitoid in the US.

Carpenter (1995) examined the influence of host species, host availability, and mating status on *I. promissorius* fecundity and oviposition. The results from this study suggest that the females budget their energy expenditures and regulate oogenesis to maximize their reproductive potential. Host size, as well as the host species, may

have contributed to differences in weight of the wasps, and contributed to differences in fecundity, longevity, and oviposition between wasps reared on *S. exigua* and *H. zea* pupae. Virgin females reared on *S. exigua* pupae laid fewer eggs than virgin females reared on *H. zea* pupae.

Studies on *Vulgicheumon brevicinctor*
and *Cryptus albitarsis*

Two *V. brevicinctor* were recovered from FAW pupae collected in 1982 from a cornfield near Tifton, GA (Pair & Gross 1989). Five *V. brevicinctor* were recovered from a sample of 300 FAW pupae collected from a corn field in Rabun County, GA, in 1993, and one *V. brevicinctor* was recovered from a sample of 3 FAW pupae collected from the same field in 1994 (J. E. C., unpublished data). *V. brevicinctor* also has been reported from other noctuids and species of other lepidopteran families (Carlson 1979). For example, Bechinski & Pedigo (1983) studied the population dynamics of the green cloverworm (*Plathypena scabra* F.) in soybeans in Iowa during 1979 and 1980. They and found that *V. brevicinctor* acted in a delayed density-dependent manner on green cloverworm pupal mortality. Pavuk & Stinner (1991) reported that *V. brevicinctor* was reared from pupae of an arctiid, *Cisseps fulvicollis* (Hübner), and pupae from a pyralid, *Ostrinia nubilalis* (Hübner).

Pair & Gross (1989) collected *C. albitarsis* in Tifton, GA, from a single sample taken November 2, 1984. Four *C. albitarsis* also were recovered from a sample of 300 FAW pupae collected from a corn field in Rabun County, GA, in 1993 (J. E. C., unpublished data). Pair & Gross (1989) reported that *C. albitarsis* had been established in a laboratory colony in Tifton, GA. *C. albitarsis* cohorts from this laboratory colony were successfully reared on an artificial diet devoid of any host components (Greany and Carpenter 1998).

Studies on Ectoparasitic Nematodes Attacking Adults
of *Spodoptera frugiperda*

Remillet & Silvain in 1982 discovered and reported an ectoparasitic nematode, *Noctuidonema guyanense* Remillet & Silvain infecting *Spodoptera androgea* (Cramer) in French Guiana. It was subsequently described as a new genus and species (Remillet & Silvain 1988) most commonly found on moths of FAW, *Spodoptera latifascia* (Walker), *S. marima* (Schaus), *Anicla infecta* (Ochsenheimer), and *Leucania* spp. (Remillet & Silvain 1988).

Rogers et al. (1990a) determined the life cycle and host range for *N. guyanense* in French Guiana. They collected moths using a white sheet illuminated by UV light, by pheromone traps, and sweeping vegetation from a variety of habitats in Northeastern French Guiana. Moths in five families, Lasiocampidae, Noctuidae, Notodontidae,

Pyralidae, and Sphingidae were naturally infested with this nematode species. Twenty-five species of Noctuidae were infected by *N. guyanense*, the hosts most commonly infected were *Lesmone formularis* (Hübner), *S. dolichos* (F.), *S. frugiperda*, and *Xanthopastis timais* (Cramer) (Rogers et al. 1990a). Using the same methodologies, Rogers et al. (1990b) determined that multiple species of *Mocis* and *Spodoptera* were parasitized by the nematode in Florida and Georgia, and it was the first record of this parasite in North America. Simmons & Rogers (1990a) determined the distribution and prevalence of the nematode in tropical Americas, occurring in northern South America, Mexico, Texas, Florida, Bermuda, most of the Caribbean basin countries, and Central America.

Since 1990, numerous studies have been conducted on this nematode including biology (Simmons & Rogers 1994; Marti & Rogers 2000), pathological effects on the host (Marti et al. 1990; Rogers et al. 1993), infestation dynamics (Rogers & Marti 1992a; Silvain & Remillet 1993; Rogers & Marti 1993b), geographical distribution (Rogers et al. 1993; Rogers et al. 1991; Simmons et al. 1991; Rogers et al. 1997; Marti et al. 2000), ecology (Silvain & Remillet 1993), population profiles (Rogers & Marti 1992a, 1994), mating behavior (Simmons & Marti 1992), prevalence (Simmons & Rogers 1990b), maintenance of colonies (Rogers & Marti 1993a, b), host range (Simmons & Rogers 1996; Rogers & Marti 1996; Marti et al. 2000), and the bionomics of host insects of *N. guyanense* (Rogers et al. 1996; Marti et al. 2000). Subsequently however, a study on the speciation in Acugutturidae shows that *N. guyanense* is limited to the lepidopteran genera *Spodoptera* and *Pseudaletia* (Marti et al. 2002).

Simmons et al. (1991) studied the seasonal chronology of the nematode in the tropical and subtropical America, and determined that host parasitism and nematode population density varied among locations and over time. Examples include higher parasitism on male moths in Grenada (77%) than in Texas (1%), and higher nematode populations at lower latitudes than higher latitudes. Simmons & Rogers (1991) also studied the dispersal and seasonal occurrence of *N. guyanense* on FAW adults in the US. They found that nematode populations and parasitism of FAW males were higher in Eastern States than in the Plains, Midwestern, and Central states, and that the percent parasitism and the number of nematodes per infested FAW changed over time at each location.

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EVALUATION OF REMOTE SENSING TO IDENTIFY VARIABILITY IN COTTON PLANT GROWTH AND CORRELATION WITH LARVAL DENSITIES OF BEET ARMYWORM AND CABBAGE LOOPER (LEPIDOPTERA:NOCTUIDAE)

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ABSTRACT

Field experiments were conducted from 2000 to 2002 in the Mississippi Delta to evaluate remote sensing technologies for identifying factors in cotton growth and development related to infestations of beet armyworm and cabbage looper. Larval defoliation of plants was monitored using remote sensing techniques including aerial and hand-held sensors as well as visual measurements of damage. Percent reflectance differed for beet armyworm infested leaves compared to uninfested leaves. In two whole field studies, more beet armyworm hits were found in zones of less vigorous and open canopy, which corresponded to lower normalized difference vegetation index (NDVI) values calculated from remotely sensed imagery. Percent light penetration of canopy was greater for plots damaged by looper larvae than for less damaged plots where looper larvae were controlled with insecticide, but NDVI values were not different.

Key Words: Insect management, beet armyworm, cabbage looper, cotton defoliators, remote sensing

RESUMEN

Se llevaron a cabo experimentos de campo desde el año 2000 al 2002 en el Delta del Mississippi para evaluar las técnicas de observación remota (remote sensing) para identificar los factores en el crecimiento y desarrollo del algodón relacionadas con las infestaciones del gusano trozador de la remolacha y el gusano medidor del repollo. La defoliación de plantas por las larvas fué monitoreada usando técnicas de observación remota incluyendo sensores aéreos y de mano y medidas visuales del daño. El porcentaje de la reflexión varió en las hojas infestadas con el gusano trozador comparado con hojas no infestadas. En dos estudios que abarcaron todo el campo, se encontraron más concentración (encuentros positivos) del gusano trozador de la remolacha en sonas donde el dosél de las plantas es abierto y vigoroso, lo cual corresponde a valores del índice de la diferencia vegetal normalizada (NDVI en inglés), más bajos calculados de las imágenes de observación remota. El porcentaje de la penetración de luz al dosél fué más alto en las parcelas dañadas por larvas del medidor que en las parcelas menos dañadas donde las larvas de medidor fueron controladas con insecticida, pero los valores de NDVI no fueron diferentes.

Beet armyworm, *Spodoptera exigua* (Hubner), is an occasional pest of cotton in the Midsouth that can become a severe pest under some environmental conditions (Leigh et al. 1996). Beet armyworm outbreaks are typically associated with high temperatures, drought conditions, and intensive insecticide regimes that eliminate natural enemies (Stewart et al. 1996). Infestations of beet armyworm in cotton also are associated with canopy development and varying levels of plant nutrients such as low levels of potassium and high levels of zinc (Parajulee et al. 1999; Graham & Gaylor 1997; Akey et al. 1990).

Cabbage looper, *Trichoplusia ni* (Hubner), is an occasional pest of cotton that only reaches damaging levels in late-season in Mississippi (Jost & Pitre 2002). High plant densities and vig-

orously growing plants are typically attractive for cabbage looper oviposition and larval densities are usually greater under these conditions (Wilson et al. 1982; Greene 1984).

Remote sensing is a promising technology that may provide early detection of localized infestations of these pests based on associated crop conditions (Allen et al. 1999). Remotely sensed data may permit reduced applications of insecticides using variable rate technology (Dupont et al. 2000). Insect pests like tarnished plant bug, have been found in abundance in vigorously growing portions of cotton fields that generally have faster fruiting rates, taller plants and/or greater canopy closure (Willers et al. 1999). These vigorous growth zones can be identified in remotely sensed imagery to target site-specific insecticide applica-

tions with variable rate technology (Dupont et al. 2000, Willers et al. 2000). Multi-spectral remotely sensed imagery of cotton fields is acquired aerially and the normalized difference vegetation index (NDVI) is calculated. The NDVI is associated with crop vigor and is a calculation of the near infrared (NIR) and red (R) wavelengths such that $NDVI = (NIR - R) / (NIR + R)$ (Willers et al. 1999). In remotely sensed imagery, NDVI values can be used to identify spatial variability in the cotton canopy. Insecticide savings of 20-50% in control of tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), can be achieved through the use of prescription application maps that are generated from classed NDVI values (DuPont et al. 2000; Sudbrink et al. 2001).

Studies to determine the utility of this technology for managing other pests are needed. For example, other researchers report that beet armyworm infests stressed or open cotton canopy zones (Stewart et al. 1996). These zones may be treatable on a site-specific basis. More information is needed to determine if those zones can be identified with remotely sensed imagery. The objective of these studies was to evaluate remote sensing technologies for identifying factors in cotton growth and development related to insect pest infestation populations including infestations of beet armyworm and cabbage looper.

MATERIALS AND METHODS

Field experiments were conducted from 2000 to 2002 on the Delta Branch Experiment Station, Stoneville, Mississippi, or the nearby (ca. 10 miles distance) satellite station at Tribbett, MS, to evaluate potential for remotely sensed data to detect cotton plant characteristics associated with infestations of leaf feeding insects such as beet armyworm and cabbage looper. These tests included grid-sampled fields as well as plot studies where varietal, insecticidal, and plant growth regulator effects on these pests in cotton were investigated. Statistical analyses were performed with ARM software (Gyllum Data Management, Inc., Brookings, SD) and correlation analyses were performed using SAS for Windows 8e (SAS Institute 1990).

Test 1 Tribbett—2000

A test was conducted at Tribbett, MS in 2000 on a 2.4 acre field (320-ft × 320-ft square) subdivided into a geometrically square 8 × 8 grid. Each grid unit was 40-ft × 40-ft square. The 64 basic units of the grid were further subdivided diagonally to create 128 sub-sample units, each a 40-ft × 40-ft × 56.6-ft right triangle.

Plots were geo-spatially mapped with a Trimble® (Trimble navigation, Sunnyvale, CA) Ag124 GPS unit. Plant development was monitored

weekly using the COTMAN expert system, which includes measurements of plant height, square shed, and nodes above white flower (NAWF) (Cochran et al. 1998). Beet armyworm damage was monitored by observations of hits per 80-row ft. Data were converted to hits per 100-row ft. for treatment decision purposes and for data analysis and presentation. A beet armyworm hit is defined as an area on a cotton leaf where a group of beet armyworm larvae feed and skeletonize the lower leaf surface, often spinning silk over the site. Treatment decision (spray or not spray) was based on the Mississippi State University Extension Service *Cotton Insect Control Guide* (Layton, 2000).

Aerial remote sensing fly-overs were made approximately every 7-14 d. Spectral reflectance data were acquired in the aerial fly-overs with a Duncan MS2100, 3-Chip Progressive Scan, Digital Smart Camera. Spectro-radiometry data were also recorded from field plots on fly-over dates and other intervening dates with a GER® 1500 spectro-radiometer (Geophysical Environmental Research Corp., Millbrook, NY).

Test 2 Stoneville—2002

Whole field observations of beet armyworm infestations were made in an 8-acre cotton field at Stoneville in late August, 2002. Imagery data (aerially acquired with equipment as described for Test 1 Tribbett 2000) were used to select paired observation sites—one in closed canopy (higher NDVI) cotton and one in open canopy (lower NDVI) cotton. Paired observations were made at fifteen locations over the field. Each observation consisted of beet armyworm hits/100 row ft. (n = 30). Means and standard errors of beet armyworm hits were calculated from data that were classed into four equal-interval categories of the NDVI values.

Test 3 Stoneville—2001

A plant growth regulator by cotton variety trial was arranged as a factorial experiment in a randomized-complete-block design replicated four times. Cotton was planted on 05/21/01. Each plot was 26.7 ft (8 rows) wide by 50 ft long. Mepiquat chloride treatments were applied on 07/20/01, 07/21/01 and 08/3/01. The two factors were (1) plant-growth-regulator treatments (PGR) (two levels, non-treated, and treated with mepiquat chloride {Pix®, 8 oz/acre, applied 2 times}), and (2) cotton varieties (four levels—Stoneville 474 [non-transgenic], Deltapine 5415 [non-transgenic], Deltapine NuCotn 33B [transgenic], and Stoneville 4691B [transgenic]). Spectroradiometry readings (GER 1500 spectro-radiometer as described for Test 1 Tribbett 2000) were taken weekly from each plot and NDVI values were calculated with these data.

The test was modified in late season after beet armyworm and cabbage looper infestations became established. Plots in each replicate were divided (without randomization and perpendicular to row direction) into two equal size plots. The south end plots were untreated and north end plots were treated with spinosad. This non-random assignment of Factor C treatments was necessary to limit potential influence of drift. The spinosad treatment was applied on 09/19/01.

The final experimental arrangement was a factorial RCB design replicated four times with three factors, (A) PGR treatment—2 levels, (B) cotton variety—4 levels, and (C) caterpillar insecticide treatment—(2 levels, untreated and treated with spinosad {Tracer®, 0.07 lb ai/acre}).

The purpose of this experimental design was to create plant growth differences with different varieties and different PGR treatments and to create different beet armyworm and/or cabbage looper infestations with different insecticide treatments, and to determine if the differences could be detected with remotely sensed data.

RESULTS

Test 1 Tribbett—2000

A beet armyworm infestation reached treatment threshold levels during August in the grid-sampled test at Tribbett in 2000. Results from spectroradiometry readings of individual leaves revealed that percent reflectance patterns were distinctive for BAW damaged leaves compared to healthy leaves (Fig. 1). Damaged leaves had lower near infrared values than the healthy leaves. Beet armyworm hits were found above treatment threshold levels in zones that had lower NDVI values calculated from aerial remote imagery (Fig. 2). The NDVI values in the gray zones in Fig. 2 were lower than NDVI values in the white zones. The image was classed into four equal interval NDVI classes. Average plant height was significantly taller with each progressively higher quartile of NDVI values. Progressively higher average numbers of BAW hits were associated with progressively lower NDVI classes (Table 1). The lower NDVI classes were associated with less vigorous plants that were shorter than those in the higher NDVI classes.

Correlation analyses revealed that there was a significant negative correlation between beet armyworm hits and NDVI value on two dates (7 & 14 August) (Table 1).

Test 2 Stoneville—2002

In late August of 2002 a beet armyworm infestation reached treatment threshold levels in the parts of the field study site at Stoneville. On 30 August 2002, aerial image-based observations re-

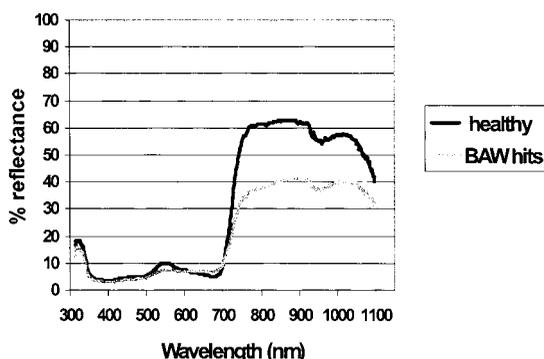


Fig. 1 Reflectance curves for leaf canopy with beet armyworm damage versus healthy canopy, Tribbett, MS, 8 August 2000.

vealed that beet armyworm hits occurred over treatment threshold levels in the two lower NDVI class zones sampled (which were associated with open or nearly open canopy) (Table 2). Sub-threshold levels of beet armyworm hits were found in samples taken in the two higher NDVI class zones. Similar observations have been made in very large commercial cotton fields at Gunnison, MS, about 60 miles north of Stoneville. Image based scouting there revealed that beet armyworm was found only in areas of lower NDVI, albeit in extremely low populations (<1%) (J.L.W., unpublished).

Correlation analysis revealed a highly significant negative relationship between beet armyworm hits and NDVI values (Table 2).

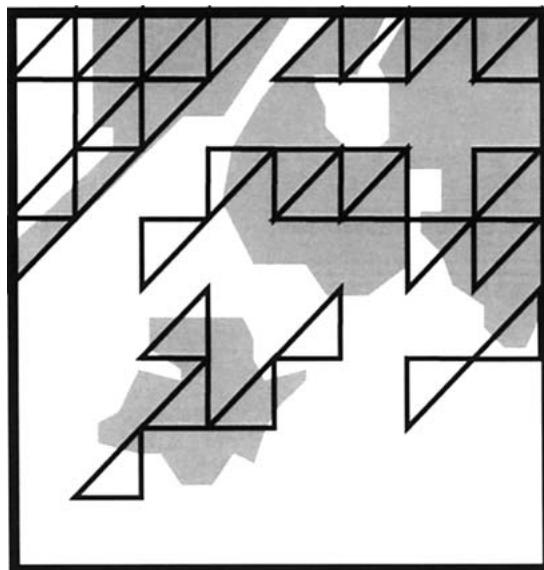


Fig. 2. Test 1 field with low (gray) and high (white) NDVI zones. Overlaid triangular sample units had beet armyworm hits above treatment threshold.

TABLE 1. NDVI CLASS VALUES FROM AERIAL REMOTE SENSING, PLANT HEIGHTS, AND MEAN NUMBER OF BEET ARMYWORM (BAW) HITS/100 FT ROW AND CORRELATIONS BETWEEN BEET ARMYWORM HITS AND NDVI, TRIBBETT, MS, AUGUST 2000.

NDVI class and range 8/7/00	n	Plant height (inches)	BAW hits/ 100ft. row 8/7/00	BAW hits/ 100ft. row 8/14/00
		Mean \pm SEM 7/26/00	Mean \pm SEM	Mean \pm SEM
Class I 0.367-0.423	15	36.60 \pm 1.04	4.67 \pm 0.55	5.42 \pm 0.51
Class II 0.423-0.479	20	40.35 \pm 1.01	3.44 \pm 0.49	4.63 \pm 0.51
Class III 0.479-0.535	40	42.58 \pm 0.65	2.78 \pm 0.38	4.03 \pm 0.35
Class IV 0.535-0.591	53	43.38 \pm 0.71	2.19 \pm 0.21	2.97 \pm 0.23

Correlation analyses					
Correlation BAW hits vs. NDVI	n	Slope	Intercept	r	P
8/7/00	128	-12.52	9.248	-0.343	<0.0001
8/14/00	128	-14.19	11.09	-0.386	<0.0001

Test 3 Stoneville—2001

Populations of beet armyworm larvae remained below treatment threshold levels at the Stoneville test in 2001. Late in the season, an infestation of cabbage looper approached economic threshold levels. There were no significant differences in numbers of cabbage looper larvae among variety or mepiquat chloride treatments and no significant interactions.

Spinosad treatments had significantly fewer cabbage looper larvae than untreated plots (Table 3). Larval feeding was measured by determining percentage light penetration through the canopy as measured by a Li-Cor® (Li-Cor, Inc., Lincoln, NE) light bar. Percent light penetration was significantly lower in spinosad treated plots than in untreated plots. This result indicates that less feeding occurred in the spinosad treated plots. However, there was no significant difference in mean NDVI between spinosad treated and untreated plots (Table 3). Thus, despite measurable

differences in looper feeding damage in this test, a difference in spectral reflectance was not detected.

DISCUSSION

Results from these experiments indicate that beet armyworm infestations were associated with lower NDVI values in remotely sensed data that represented zones of open and/or stressed canopy. This association may be useful in the development of future sampling plans or site-specific management techniques that direct insecticide applications for beet armyworm at lower NDVI zones in a field.

The remotely sensed spectral reflectance data did not detect crop damage by cabbage looper larvae despite measurable differences in light penetration between infested (damaged) and sprayed (less damaged) canopy. This illustrates the difficulty of detection via remote sensing of insect damage, even visually observable leaf feeding, before it is too late for corrective action. Additional

TABLE 2. NDVI CLASS VALUES FROM AERIAL REMOTE SENSING AND MEAN NUMBER OF BEET ARMYWORM (BAW) HITS/100' ROW AND CORRELATION BETWEEN BEET ARMYWORM HITS AND NDVI, STONEVILLE, MS, 30 AUGUST, 2002.

NDVI class and range	n	BAW hits/ 100 ft. row			
		Mean \pm SEM			
Class I <-0.097>-0.024	3	5.67 \pm 0.67			
Class II 0.024-0.145	7	4.71 \pm 0.42			
Class III 0.145-0.266	10	2.90 \pm 0.94			
Class IV 0.266-0.387	10	0.50 \pm 0.22			

Correlation analyses					
Correlation	n	Slope	Intercept	r	P
BAW hits vs. NDVI	30	-16.794	6.074	-0.774	<0.0001

TABLE 3. EFFECT OF SPINOSAD ON A CABBAGE LOOPER INFESTATION, PERCENT LIGHT PENETRATION IN PLANT CANOPY, AND NDVI VALUES FROM HAND-HELD SPECTRO-RADIOMETRY, FIELD 11, STONEVILLE, MS, 2001.

Treatment	Mean looper larvae/6 ft row 24-Sep-01	% Light penetration 01-Oct-01	NDVI value 01-Oct-01
Control	11.7	7.85	0.7623
Spinosad	2.7	5.34	0.7788
LSD	1.9	1.42	0.0330
Prob (F)	0.0001*	0.0001*	0.488 ns

*Indicates significant difference (P = 0.05) in Factorial test.

study will be needed to determine if cabbage looper infestation can be associated with plant characteristics that are detectable via remote sensing techniques.

Image-based scouting through characterization of canopy development for beet armyworm may be useful in site-specific management of this cotton pest. Further research is required to elucidate the relationship of lower NDVI levels to beet armyworm hits and develop it into a useful sampling and site-specific management plan.

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LARVAL DEVELOPMENT OF *SPODOPTERA EXIGUA* (LEPIDOPTERA: NOCTUIDAE) LARVAE ON ARTIFICIAL DIET AND COTTON LEAVES CONTAINING A *BACILLUS THURINGIENSIS* TOXIN: HERITABLE VARIATION TO TOLERATE CRY1AC

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ABSTRACT

Studies were conducted to determine if beet armyworms, *Spodoptera exigua* (Hübner), possess the genetic variation necessary to respond to selection for improved tolerance of the *Bacillus thuringiensis* Berliner (Bt) toxin Cry1Ac. *Spodoptera exigua* individuals that pupated earliest when fed the Cry1Ac diet (ca. the first 20% to pupate) produced offspring that developed significantly faster on the Cry1Ac diet than their parental-control strain. In addition, after two generations of selection, the selected population reached pupation 2 d faster than the Parental population. The selected group also developed significantly faster on transgenic-Bt cotton leaves (cv. NuCOTN 33B) than the Parental strain. Individuals selected to more rapidly develop on media containing Cry1Ac developed no more rapidly on artificial diet containing Cry2Aa than the parental, control colony of *S. exigua*.

Key Words: *Spodoptera exigua*, *Bacillus thuringiensis*, insecticide resistance, heritability, Cry1Ac

RESUMEN

Se llevaron a cabo estudios para determinar si el gusano trozador de la remolacha, *Spodoptera exigua* (Hübner), posee la variación genética necesaria para responder a la selección para la tolerancia mejorada de toxina Cry1Ac de *Bacillus thuringiensis* Berliner (Bt). Los individuos de *Spodoptera exigua* que se empuparon más temprano cuando fueron alimentados de una dieta de Cry1Ac (ca. los primeros 20% que se empuparon) produjeron descendientes que se desarrollaron significativamente más rápidos con la dieta de Cry1Ac que el grupo control de la raza de su pariente. Además, después de dos generaciones de selección, la población seleccionada se empuparon 2 días más rápida que la población pariente. El grupo seleccionado también se desarrolló significativamente más rápido en las hojas de algodón transgénicas-Bt (cv. NuCOTN 33B) que la raza Pariente. Los individuos seleccionados para desarrollarse más rápidos en un medio conteniendo Cry1Ac no se desarrollaron más rápidamente en la dieta artificial con Cry2Aa que en la colonia control pariente de *S. exigua*.

Cotton varieties containing a gene from *Bacillus thuringiensis* (Berliner) (Bt) that expresses the insecticidal protein Cry1Ac have been commercially available since 1996. The Cry1Ac-expressing varieties of Bt cotton were developed primarily to control the tobacco budworm, *Heliothis virescens* F. and the pink bollworm, *Pectinophora gossypiella* (Saunders). The abilities of different species of insects feeding on cotton to tolerate Bt proteins will play an important role in determining how Bt cotton influences the population dynamics of these pests.

Spodoptera exigua (Hübner), a secondary pest of cotton, is more tolerant of Cry1Ac than the tobacco budworm (Gould & Tabashnik 1998). Although *S. exigua* can survive initial encounters with cotton tissue expressing Cry1Ac, its larval development is delayed. Delayed larval development not only slows the buildup of population

size in this species, but it may have the potential to increase its generation time. One important step is to determine if the genetic potential exists in *S. exigua* to become more tolerant of Cry1Ac, i.e., develop more rapidly on tissue containing Cry1Ac. The purpose of this research is to determine if there is genetic potential in this species to more rapidly finish larval development when feeding on food sources containing Cry1Ac. In addition, the performance of *S. exigua* on a second Cry protein is also investigated.

MATERIALS AND METHODS

Insect Colony and Diet

The *S. exigua* colony used during this study is maintained at the USDA-ARS, Southern Insect Management Research Unit, Stoneville, MS. Lar-

vae were fed a standard artificial diet developed for Lepidoptera (Raulston & Lingren 1972). Cry1Ac diet was prepared by mixing a concentrated stock solution of MVPII powder into 300-500 ml batches of artificial diet to obtain a final concentration of 1.0 $\mu\text{g}/\text{ml}$ Cry1Ac (approx.). A single neonate larva was placed into a 30-ml cup containing approx. 10 ml of Cry1Ac diet. This concentration (6.8 $\mu\text{g}/\text{g}$ dry weight of diet) is comparable to reported amounts of Cry1Ac present in cotton tissue (6.7 $\mu\text{g}/\text{g}$ dry weight of diet; Greenplate 1999) during the latter part of the growing season (116 d after plating). Larvae from all test groups were also placed on non-Cry1Ac diet as a control. Environmental conditions for these tests were $27 \pm 1^\circ\text{C}$, 45-60% RH, and a photoperiod of 14:10 (L:D).

For two generations, individuals that completed larval development more rapidly when feeding on Cry1Ac diet were selected based on the number of days required to reach pupation (≤ 16 d; Fig. 1, "Selected" colony). In addition to testing the Selected colony on Cry1Ac diet, its performance was also assessed on non-Cry1Ac diet. The Parental strain was always tested on both types of diet at the same time as the selected colony.

First and Second Generations

During the first generation, the number of days to pupation for each tested individual from the Parental colony was recorded. Parental-colony larvae were tested on both Cry1Ac ($N = 510$) and non-Cry1Ac diets ($N = 60$). The pupae resulting from individuals tested on Cry1Ac diet were placed into three groups: (1) the "Selected" group was composed of individuals that had pupated by 14-16 d on Cry1Ac diet; (2) an "Intermediate" group was composed of individuals that pupated by 17-20 d on Cry1Ac diet; and (3) a "Slow" group was composed of individuals that pupated after 21 d of exposure to Cry1Ac diet. Adults from each

group were mated *inter se* to produce their second-generation progenies. The larval developments (days to pupation) of these offspring were compared among the above groups and also to the Parental colony on both Cry1Ac ($N > 200$ per group) and non-Cry1Ac diets ($N = 30$ per group). In addition, larvae from the two extreme groups ("Selected" and "Slow") and the Parental strain were weighed at 7 d. The weights were used as another measure of larval development on Cry1Ac and non-Cry1Ac diets.

Differences between groups for the number of days to pupation were analyzed via non-parametric statistics. Comparisons between two groups (first generation) were made using Wilcoxon rank-sum tests (SAS 1995). Comparisons of >2 groups (second generation) were made with Kruskal-Wallis ANOVA (SAS 1995). When Kruskal-Wallis results indicated significant differences, means were separated via pairwise-comparisons among the groups using the Wilcoxon rank-sum tests. Bonferroni adjustments were made in the significance levels for follow-up tests to control the overall Type I error at $P = 0.05$ ($n = 4$ groups, therefore significance was set at $P < 0.008$).

Third Generation

Third-generation individuals from the Selected colony were tested on Cry1Ac and non-Cry1Ac diets and compared with the unselected, Parental colony. As with the previous generations, the number of days to pupation was recorded for each individual. Comparisons between the Selected and Parental groups were made via Wilcoxon rank sum tests (SAS 1995).

Fourth Generation

Most of the third-generation larvae from the Selected group were fed non-Cry1Ac diet in order to not put the colony through another bottleneck and also to increase the size of the colony for the fourth generation of testing on plant tissue. As a consequence, parents of the fourth-generation larvae from the Selected group underwent no selection for improved tolerance of Cry1Ac. During the fourth generation, larvae from the Parental colony and Selected colony were assayed on transgenic-Bt cotton leaves (cv. NuCOTN 33B) and non-Bt cotton leaves (cv. DP5415). Growth of larvae on both types of cotton leaves was evaluated via 10-d weights.

To test for differences in larval growth between the Selected and Parental groups on leaves of Bt and non-Bt cotton, a single leaf from the upper canopy of cotton plants was placed into a circular leaf cup. Five larvae were placed into each cup. To help control for environmental heterogeneity in the performance of the cotton, tests were

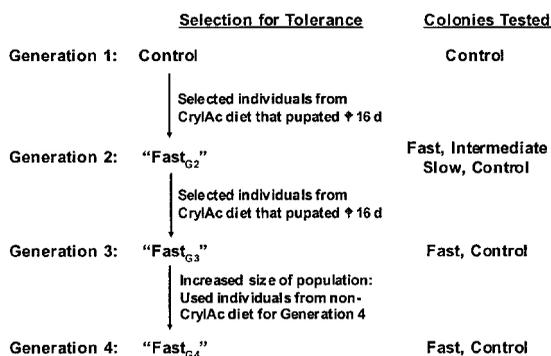


Fig. 1. Mating design for the selection and tests of *S. exigua* individuals and colonies more tolerant of Cry1Ac.

blocked by the location where the cotton was grown. NuCOTN 33B and DP5415 were planted in four sets of paired plots. For each block, leaves were collected from the same set of paired plots and replaced every 2 d. Ten cups per insect group per cotton variety were randomized on a tray for each block. Two blocks were set up with the first egg clutch from both colonies, while the remaining two blocks were set up the next day with larvae from the second egg clutch. As a consequence, egg clutch and block are not independent of each other. In our ANOVA, block effects and cups nested within (block \times cotton variety) treatments were considered random sources of error. Insect group was considered a fixed source of variation. Proc Mixed was used to analyze the log-transformed weights and estimated the denominator degrees of freedom based on Satterthwaite's approximation (Littell et al. 1996).

Performance on Cry1Ac and Cry2Aa

The duration of larval development for larvae from the Selected and Parental colonies was compared on non-Bt, Cry1Ac, and Cry2Aa diets. The duration of larval development was measured as the number of days required to finish larval development (days to pupation). The purpose was to determine if the performance of colonies when feeding on Cry1Ac and Cry2Aa was correlated.

Cry1Ac diet was prepared as described above. Cry2Aa was supplied by B. Moar, Auburn University. A concentration of 10 μ g per ml Cry2Aa was chosen for investigating larval development. In other work, the expression of Cry2Ab, a similar protein to Cry2Aa, in BollgardII cotton was approx. 10 \times greater than the expression of Cry1Ac. The Cry1Ac concentration was increased 10-fold to determine our concentration of Cry2Aa used in this experiment.

RESULTS

Generations 1 and 2

The development of *S. exigua* larvae was significantly different on Cry1Ac compared with non-Cry1Ac diet (Wilcoxon test $P < 0.0001$). Days to pupation for the Parental colony during the first generation ranged from 15-28 d when larvae were reared on 1.0 μ g/ml Cry1Ac diet. All individuals had pupated by 14 d on the non-Cry1Ac diet.

Individuals from the Selected group produced second-generation offspring that pupated significantly earlier on the Cry1Ac diet than individuals from the Parental, Intermediate, and Slow groups (Fig. 2A; K-W ANOVA $H = 149.94$; $df = 3$; $P < 0.0001$). All groups differed significantly in their development on the toxic diet ($P < 0.0001$ for all comparisons). Individuals from the Selected group pupated ca. 1 d earlier than the larvae from the

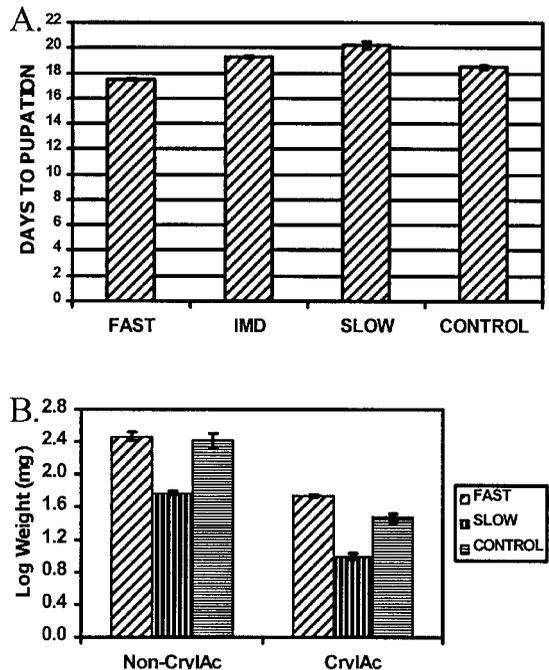


Fig. 2. Second-generation tests of *S. exigua* groups. (A) Days to pupation for mating groups feeding on Cry1Ac diet and (B) average (\pm SE, mg) log weight of mating groups on non-Cry1Ac and Cry1Ac diets. Bars with the same letter do not differ significantly as determined by Wilcoxon tests (A) and analysis of least-squared means (B).

Parental colony. On non-Cry1Ac diet there were also significant differences among groups in their days to pupation ($H = 79.93$; $df = 3$; $P < 0.0001$). Greater than 90% of the larvae from the Selected, Intermediate, and Parental groups had pupated by 14 d. The only group to significantly differ from the others was the Slow group. Individuals from the Slow group took significantly longer to pupate (mean \pm SE = 13.90 \pm 0.10, 14.00 \pm 0.08, 16.14 \pm 0.08, and 14.77 \pm 0.10 d, for Selected, Intermediate, Slow, and Parental, respectively).

The 7-d log weights of larvae supported the days to pupation results during the second generation. There were significant differences among the log weights (mg) of the second-generation colonies on non-Cry1Ac diet ($F = 158.43$; $df = 2, 55$; $P < 0.0001$) and Cry1Ac diet ($F = 155.15$; $df = 2, 203$; $P < 0.0001$). On both diets the Slow group was significantly smaller than the Parental and Selected group (Fig. 2B). However, the Selected group grew significantly faster on the Cry1Ac diet than the Parental group, but there was no difference in growth on the non-Cry1Ac diet (Fig. 2B). The ratios of the average log weight on Cry1Ac relative to non-Cry1Ac diet were 0.706, 0.607, and 0.560 for the Selected, Parental, and Slow groups, respectively. In addition, the percentage differences

for the log weight of groups on Cry1Ac relative to non-Cry1Ac were -29.43, -39.30, and -44.02% for the Selected, Parental, and Slow groups, respectively.

Generation 3

The improved growth of the Selected group continued into the third generation. During the third generation, the Selected group pupated significantly earlier than the Parental group when larvae were fed Cry1Ac diet ($P < 0.0001$; 16.24 ± 0.14 vs. 18.75 ± 0.15 d for the Selected and Parental groups, respectively). Most individuals (>90%) from both groups pupated by 14 d on the non-Cry1Ac diet ($P > 0.6$).

The mean days to pupation significantly differed among generations ($F = 46.65$; $df = 2, 445$; $P < 0.0001$). All pair-wise comparisons of least-squared means for generations differed from each other (all Bonferroni-adjusted P 's < 0.0001). The percentage of the total individuals feeding on Cry1Ac diet that pupated ≤ 15 d increased with each generation of selection (2.6, 6.2, and 33.3% for generation 1, 2, and 3, respectively). The mean number of days to pupation also decreased after each episode of selection (Fig. 3).

Generation 4

During the fourth generation, the Selected colony was compared with the Parental colony in 10-d tests involving leaves of NuCOTN 33B (Bt cotton) and DP5415 (non-Bt cotton). Two-way ANOVA found significant effects of cotton variety ($F = 84.90$; $df = 1, 77.7$; $P < 0.0001$), BAW colony ($F = 17.06$; $df = 1, 647$; $P < 0.0001$) and variety \times colony ($F = 10.21$; $df = 1, 647$; $P = 0.0015$) on larval weights. Tests of least-squared means (Slice option of lsmeans statement, Proc Mixed) found no significant and significant differences between larval weights of Selected and Parental colonies when they were feeding on non-Bt leaves (DP5415 $F = 0.45$; $df = 1, 646$; $P = 0.5046$) and Bt leaves (NuCOTN 33B $F = 26.30$; $df = 1, 648$; $P < 0.0001$), respectively. Larvae from the Selected strain were significantly larger than individuals

from the Parental strain after 10 d of feeding on Bt cotton leaves.

During the leaf tests, comparisons between the Selected and Parental groups were also made on artificial diets. There were no differences between the two groups after 11 d of feeding on non-Cry1Ac diet ($P = 0.099$, with slightly better growth in Parental group). However, larvae from the Selected group were significantly larger than larvae from the Parental group after feeding for 11 d on Cry1Ac diet (average weights = 151.3 and 75.3 mg, for Selected and Parental, respectively; $F = 37.00$; $df = 1, 10.3$; $P < 0.0001$).

Cry1Ac and Cry2Aa Tests

Larval development was influenced by larval diet ($F = 157.68$; $df = 1, 331$; $P < 0.0001$; Fig. 5) and the interaction between larval diet and *S. exigua* colony ($F = 4.37$; $df = 2, 331$; $P = 0.0134$). Larvae from the selected colony pupated significantly earlier than larvae from the Parental colony when exposed to Cry1Ac diet ($F = 9.55$; $df = 1, 331$; $P = 0.0022$; Fig. 5). However, there were no significant differences in the number of days to reach pupation between the Parental and selected colonies when larvae fed on non-Bt diet or Cry2Aa diets ($P > 0.6$; Fig. 5).

DISCUSSION

Spodoptera exigua had sufficient genetic variation to respond to selection for improved tolerance of Cry1Ac. After two generations of minimal selection, the Selected group pupated approximately 2 d earlier on Cry1Ac diet than the Parental strain. The better growth of the Selected group on the leaves of Bt cotton supports that the Selected colony had become more tolerant of Cry1Ac

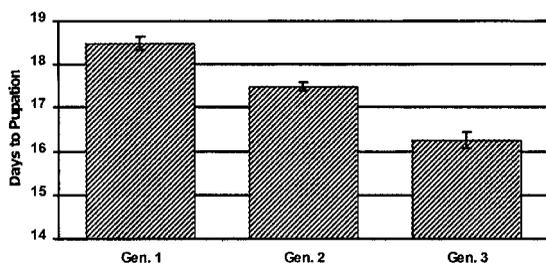


Fig. 3. Mean days to pupation (\pm SE) during after each generation of selection

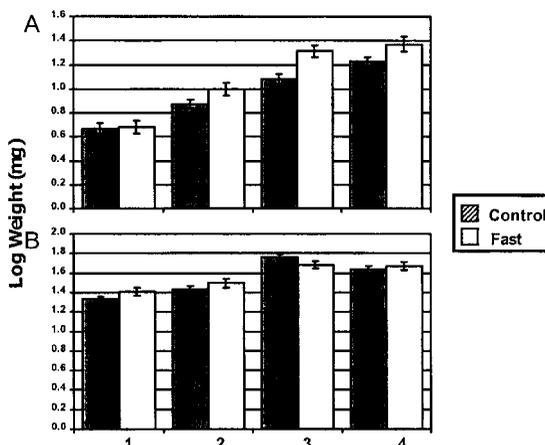


Fig. 4. Mean log weight (\pm SE, mg) of the Selected and Parental groups when tested on Bt cotton leaves (A) and non-Bt cotton leaves (B) during generation 4.

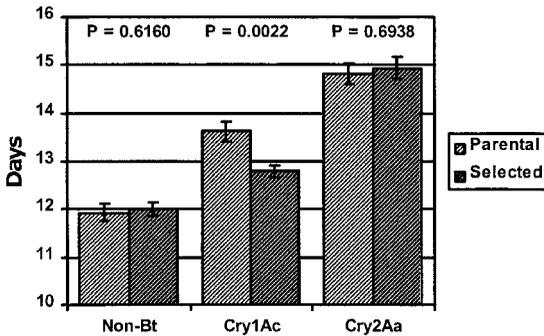


Fig. 5. Mean days to pupation (\pm SE) when the Selected and Parental colonies are exposed to artificial diets containing the no Bt proteins, Cry1Ac and Cry2Aa.

relative to the parental colony. In addition, the rapid response to selection suggests that there is little recessive gene action for development when larvae are exposed to tissue expressing Cry1Ac.

The growth of larvae on conventional cotton tissue was significantly more rapid than the growth of selected larvae on Cry1Ac-expressing tissue. There is a potential for assortative mating of adults based on the relative growth rates of larvae while feeding on expressing and non-expressing cotton tissue. The degree of assortative mating will be dependent on the overlap of larval development on the two types of tissue. As the population becomes more tolerant of the Cry1Ac tissue, there should be greater overlap in the development of larvae feeding on non-Cry1Ac tissue. Although there is little recessive gene action, one consequence of the greater overlap in larval development and its reduction in positive assortative mating will be to slow the evolution of improved growth when larvae are feeding on Cry1Ac-expressing tissue.

Unlike conventional insecticides used to control late-season populations of *S. exigua*, the con-

tinuous expression of Cry1Ac in cotton leaves may create unwanted selection for improved tolerance in field populations that are below economically-damaging densities. However, the lack of a significant relationship between larval development on Cry1Ac and Cry2Aa will delay the response to selection for improved growth on tissue expressing these two toxins or Cry proteins related to these proteins. Stacked varieties may therefore play an important role in the evolution of ecological characters that will influence population development and generation time.

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ARTHROPODS ASSOCIATED WITH ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA*, IN SOUTH FLORIDA, USA

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ABSTRACT

Melaleuca quinquenervia (Cav.) S. T. Blake, the broad-leaved paperbark tree, has invaded ca. 202,000 ha in Florida, including portions of the Everglades National Park. We performed prerelease surveys in south Florida to determine if native or accidentally introduced arthropods exploit this invasive plant species and assess the potential for higher trophic levels to interfere with the establishment and success of future biological control agents. Herein we quantify the abundance of arthropods present on the above-ground portions of saplings and small *M. quinquenervia* trees at four sites. Only eight of the 328 arthropods collected were observed feeding on *M. quinquenervia*. Among the arthropods collected in the plants adventive range, 19 species are agricultural or horticultural pests. The high percentage of rare species (72.0%), presumed to be transient or merely resting on the foliage, and the paucity of species observed feeding on the weed, suggests that future biological control agents will face little if any competition from pre-existing plant-feeding arthropods.

Key Words: Paperbark tree, arthropod abundance, *Oxyops vitiosa*, weed biological control

RESUMEN

Melaleuca quinquenervia (Cav.) S. T. Blake ha invadido ca. 202,000 ha en la Florida, incluyendo unas porciones del Parque Nacional de los Everglades. Nosotros realizamos sondeos preliminares en el sur de la Florida para determinar si los artrópodos nativos o accidentalmente introducidos explotan esta especie de planta invasora y evaluar el potencial de los niveles tróficos superiores para interferir con el establecimiento y éxito de futuros agentes de control biológico. En cuatro sitios, nosotros cuantificamos la abundancia de artrópodos presentes en las porciones sobre el terreno de los renuevos y pequeños arboles de *M. quinquenervia*. Solamente ocho de los 328 artrópodos recolectados fueron observados alimentándose en la *M. quinquenervia*. Entre los artrópodos colectados en las áreas no nativas de la planta, 19 especies son plagas agrícolas ó de hortalizas. El alto porcentaje de especies raras (72.0%), presumidos de ser transeúntes o meramente descansando en el follaje, y la escasez de especies observadas alimentándose de la maleza, sugiere que los futuros agentes de control biológico enfrentarán poca o ninguna competencia de los artrópodos herbívoras ya presentes en la planta.

Melaleuca quinquenervia (Cav.) S.T. Blake, the broad-leaved paperbark tree, was introduced into south Florida during the late 1800s (Thayer & Bodle 1990). Although threatened in its native range along the east coast of Australia and a few nearby South Pacific islands, life history characteristics of *M. quinquenervia* (melaleuca) combine with favorable ecological characteristics of Everglades habitats to make this tree an explosive weed in south Florida (Meskimen 1962; Myers 1983; Balcianas & Center 1991; Hofstetter 1991). Currently, melaleuca occurs on about 202,000 ha of Florida wetlands (Bodle et al. 1994) and has historically spread at a rate of about 2,850 ha/yr (Center et al. 2000). The negative impacts of melaleuca on native flora and public health problems have been documented (Di Stefano & Fisher 1983; Myers 1983; Molnar et al. 1991; Bodle et al. 1994). Diamond et al. (1991), for instance, determined that if unchecked, potential losses to the Florida economy as a result of this invasive tree could reach \$169 million annually.

Melaleuca infested areas can be restored through removal of existing trees, followed by measures to preempt reinvasion and subsequent recruitment. Conventional control tactics combine mechanical and chemical means to eliminate seedlings, saplings, entire stands of mature trees, or isolated plants in sensitive areas (Stocker & Sanders 1981; Bodle et al. 1994). However, biological attributes of this weed necessitate repeated mechanical and chemical treatments, which impose an accumulation of negative impacts on non-target organisms, including endangered plants. These adverse impacts limit the frequent use of such methods. In contrast, classical weed biological control has been described as the most ecologically benign tactic for controlling exotic pests (McEvoy & Coombs 1999) and has been considered a desirable addition to conventional methods (Browder & Schroeder 1981; Bodle et al. 1994).

Development of a weed biological control program typically proceeds in a stepwise fashion, including: selection of a natural enemy, risk

analysis, release, monitoring establishment, and finally assessing the effectiveness and ecological impact of the introduced biological control agent (Harris 1975; McEvoy & Coombs 1999). An often recommended initial phase in a classical weed biological control program includes surveys of herbivores associated with the invasive weed in the new (adventive) geographic range (Harris 1975; Olckers & Hulley 1995). Such surveys are intended to identify herbivores already exploiting the weed and to ascertain whether niche competition could influence agent establishment and impact (Harris 1971). Although surveys for natural enemies were performed in Australia during 1987 to 1991 (Balciunas et al. 1995), surveys of arthropods associated with melaleuca in its adventive range had never been done. Failure to perform such surveys could increase costs due to wasted effort associated with selecting, screening and releasing herbivores that may already be present, having accompanied the invasive weed upon introduction or thereafter. Therefore, specific objectives of this study were: 1) assess the current abundance of arthropods associated with melaleuca in south Florida, 2) determine if native herbivores are exploiting the invasive plant, 3) determine if co-evolved natural enemies from the native range inadvertently accompanied melaleuca into south Florida, and 4) inventory those higher trophic levels associated with the plant that could potentially interfere with the establishment or impact of introduced biological control agents.

MATERIALS AND METHODS

Arthropod surveys were performed at four locations in south Florida. Site 1 was located near Ft. Lauderdale, Broward Co., FL (N26.05606 and W80.25168). The site was a 0.5 ha field consisting of 2 to 5 m tall trees occurring at a plant density of ca. 21,560 trees/ha. In general, melaleuca trees were growing in high organic soils typical of reclaimed 'glades' systems. Although melaleuca was the dominant species, other plants commonly occurring in the site included *Blechnum serrulatum* Rich., *Ampelopsis arborea* (L.) Koehne, *Vitis aestivalis* Michx., and *Ludwigia peruviana* (L.) H. Hara.

Site 2 was located under a power line right-of-way near Weston, Broward Co., FL (N26.035483 and W80.43495). Prior to 1997 land managers cut melaleuca trees near their bases, resulting in multi-stemmed branches re-growing from the stumps. The survey area was ca. 0.5 ha and trees were 2-5 m tall, occurring at a density of 2,517 trees/ha. The site was swale-like with common vegetation other than melaleuca including: *Sagittaria lancifolia* L., *Cladium jamaicense* Crantz, and *Andropogon glomeratus* (Walt.) B.S.P. (Anonymous 1990).

Site 3 was located near Estero, Collier Co., FL (N26.4255 and W81.81033) and consisted of an 8 ha area of drained wetland converted to pasture.

To suppress melaleuca growth, land managers mowed trees at ca. 6-month intervals, resulting in coppices 0.5-2 m in height. These coppicing clumps formed a dense, nearly continuous canopy of leaves with 4,406 clumps/ha. In contrast to the previous sites, the soil type was primarily sand, consistent with an invaded pine flatwoods habitat type (Anonymous 1990). Other than melaleuca, the subdominant vegetation included *Ludwigia* sp., *Centella asiatica* (L.) Urb., *Rhynchospora globularis* (Chapm.) Small, *Rhynchospora eximia* (Nees) Boeck., and *Rhynchospora filifolia* Gray.

Site 4 consisted of a 1 ha area within historically mesic flatwoods in the Picayune Forest, Collier Co., FL (N26.10478 and W81.63392) (Anonymous 1990). A fire burned much of the melaleuca dominated areas during June 1998, resulting in recruitment of 129,393 trees/ha composed of primarily small 1-2 m tall saplings, interspersed with an occasional large, mature tree. *Pinus elliottii* Engelm. and a parasitic (dodder-like) species growing on the melaleuca were the only other common vegetation.

Surveys were conducted monthly at each site from November 2000 through June 2001. Sites were surveyed between 10 a.m. and 2 p.m. on days without precipitation. To survey arthropods associated with melaleuca canopies, we swept foliage, and occasionally trunks, with a 90-cm-diameter sweep net. One sample consisted of 100 sweeps in a 180° sweeping motion spaced ca. 1.0 m apart along a randomly selected 100 m transect. Four samples along separate transects were collected each month. The contents of the net after 100 sweeps were emptied into a 3.78 liter sealable plastic bag and frozen at -19 (±1) °C until processed. Arthropods were then separated from plant material, sorted by morphological types, and stored in 70% ethanol.

One limitation of our sweep sampling method included collecting arthropods that were not closely associated with melaleuca, but were transients, merely resting on the plant foliage or disturbed from understory vegetation while sampling. Additionally, this method was biased towards those species that are poor fliers or slow to disperse from a disturbance and, unlike previous Australian surveys, endophages were not included. Therefore, caution should be used when drawing inferences from these data due to the unknown relationships between some of these arthropods and melaleuca. For this reason, a minimum of two observers searched for direct herbivory on the above ground portions of melaleuca trees for 30 min./month at each site. Arthropods observed feeding on melaleuca are reported independently from those collected in sweep samples.

For each species collected, species abundance per site was calculated for the entire survey period by first averaging the number of specimens from the four monthly samples and then averag-

ing among all sample dates. Average species abundance among all sites was determined by total specimens collected throughout the entire survey (rare = 1-5 specimens, occasional = 6-10 specimens, common = >10 specimens). Occasionally, arthropods were collected by hand to facilitate identification. Where possible, arthropods were identified to species. Identifications that could not be confirmed are indicated by "poss." (possibly) before the scientific name. Some Diptera were not sent for identification because specialists were not available or specimens were damaged and lacked key identifying features. Such specimens were combined into an "unidentified spp." group and the number of morphological types is denoted in parentheses. All morphological types, except for immatures that could be associated with their adult forms, were included in the total species count.

All specimens, except formicids, were submitted to and deposited at the Florida State Collection of Arthropods (FSCA, Division of Plant Industry (DPI), Gainesville, FL) for identification and incorporated into their taxonomic database. Most formicids were identified and retained by L. Davis at the Fire Ant Unit, Agricultural Research Service, USDA, Gainesville, FL. A few formicids were identified by M. Deyrup at the Archbold Biological Station, Lake Placid, FL. Several dipteran specimens were identified at the Systematic Entomology Laboratory, Agricultural Research Service, USDA, Beltsville, MD.

RESULTS AND DISCUSSION

Surveys of herbivores associated with an invasive plant in its adventive range are often recommended as a prelude to a weed biological control project (Harris 1975). Historically, scientists have ignored this recommendation, possibly due to the supposition that native herbivores are already suppressing the weed to the greatest level possible. In contrast, native arthropods can cause considerable damage to non-indigenous weeds (Newman et al. 1998). The native weevil, *Euhrychiopsis lecontei* Deitz, for instance, shows promise for control of Eurasian watermilfoil, *Myriophyllum spicatum* (L.) (Newman & Beisoer 2000). In addition to natives, co-evolved herbivores and diseases may also be accidentally introduced from the plant's native range. The biological control agents *Megastigmus aculeatus* (chalcid wasp) and *Phyllocoptes fructiphilus* (an eriophyoid mite), for example, were collected in West Virginia during surveys of arthropods associated with the exotic weed *Rosa multiflora* (Thunb.). The eriophyoid mite, and the virus it transmits, is considered the most effective agent for the suppression of *R. multiflora* (Amrine 1996).

In its adventive range, however, it appears that melaleuca has not acquired native herbivores at

sufficient densities to cause appreciable damage to trees in south Florida. For instance, of the 18 orders, 117 families, and 328 species collected in this study, only 54 species were classified as common and 33 species were classified as occasional (Tables 1 and 2). Of the most commonly occurring species, 33 (66.7%) were predators or detritivores (Table 2), and 11 (20.4%) were herbivores (Table 1). Both adult and immature stages of *H. coagulata*, the glassy-winged sharpshooter, were observed on melaleuca, suggesting that melaleuca may serve as an alternative host for this insect. However, during the sampling period none of these arthropods were directly observed feeding on melaleuca. Furthermore, out of 409 herbivorous arthropods found attacking melaleuca in Australia, none were found on melaleuca in south Florida indicating that no co-evolved natural enemies accompanied melaleuca into south Florida upon introduction or thereafter (Balciunas et al. 1995). The most intuitive explanation for these findings is probably due to the fact that all known importations of the invasive tree were in the form of seed (F. A. Dray, pers. comm.).

In contrast, we have observed several arthropod species feeding on melaleuca that were never recovered in the sweep samples. Both early and late instars of the polyphagous saddleback caterpillar, *Sibile stimulea* (Clem.), were observed feeding on mature melaleuca leaves at Site 3. Larvae of the caterpillar were concentrated on a single sapling, defoliated much of the tree, and were only present during late winter. After inspection of a single damaged sapling (5 cm diam), larvae of the generalist cerambycid *Neoclytus cordifer* (Klug) were also collected, allowed to pupate and successfully emerged as adults (2 males and 1 female). Two phytophagous mites, *Oligonychus coffeae* (Nietner) and *Brevipalpus obovatus* Donnadieu, were observed feeding and developing large (>100 individuals), although isolated populations. Populations of these generalist mites occurred on mature leaves and were only observed once. The Florida red scale, *Chrysomphalus aonidum* L., the stellate scale, *Vinsonis stellifera*, and an unidentified *Coccus* sp. often co-occurred on mature Melaleuca leaves. Although the scale occurred in surprisingly high densities (>10 per leaf), no apparent foliar damage was visible. Two polyphagous aphids, *Aphis gossypii* Glover and *Toxoptera aurantii* (Boyer de Fonscolombe), were observed feeding on stems of developing branches. Infestations of both polyphagous aphids were slight (<50 individuals per plant). Although these arthropod species were observed feeding on melaleuca, no damage was visible. These observational findings suggest that, unlike some invasive plants that can be stressed by native arthropods in the adventive range, the arthropod community currently associated with melaleuca provides little if any suppressive effect on the exotic tree. The pau-

TABLE 1. HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Coleoptera												
Aderidae												
<i>Ganascus ventricosus</i> LeConte	0.03 (0.09)	—	—	0.03 (0.09)	R	5	—	—	12	H	N	
Anthicidae												
<i>Vacusus vicinus</i> (LaFerte-Senecteere)	0.03 (0.09)	—	—	—	R	5	—	—	—	H	N	
Anthribidae												
<i>Trignorohinus</i> sp.	0.03 (0.09)	—	—	—	R	11	—	—	—	H	N	
Bruchidae												
<i>Sennius fallax</i> (Boheman)	—	0.03 (0.09)	—	—	R	—	3	—	—	H	N	
Buprestidae												
<i>Taphrocerus puncticollis</i> Schwarz	0.19 (0.26)	—	—	—	O	3-6	—	—	—	H	N	
Cantharidae												
<i>Chauliognathus marginatus</i> (Fabricius)	—	0.03 (0.09)	—	—	R	—	6	—	—	H	N	
Chrysomelidae												
<i>Altica</i> sp. A	—	—	0.03 (0.09)	0.03 (0.09)	R	—	—	11	12	H	N	
<i>Altica</i> sp. B	—	0.03 (0.09)	—	—	R	—	6	—	—	H	N	
<i>Bassareus brunnipes</i> (Olivier)	0.44 (0.90)	—	—	—	C	5,6	—	—	—	H	N	
<i>Chrysomela scripta</i> Fabricius	—	—	0.03 (0.09)	—	R	—	—	3	—	H	N	
<i>Graphopus curtipennis</i> Blake	—	—	—	0.03 (0.09)	R	—	—	—	1	H	N	
<i>Lexiphanes saponatus</i> (Fabricius)	—	0.03 (0.09)	—	—	R	—	6	—	—	H	N	
<i>Ophraella notulata</i> (Fabricius)	0.09 (0.19)	—	—	—	R	4,6	—	—	—	H	N	
<i>Paria</i> sp.	—	—	—	0.03 (0.09)	R	—	—	—	6	H	N	
Curculionidae												
<i>Auletes</i> sp.	—	0.06 (0.18)	—	—	R	—	6	—	—	H	N	
<i>Diaprepes abbreviatus</i> (L.)	0.03 (0.09)	—	—	—	R	4	—	—	—	H	E	*
<i>Listronotus cryptops</i> (Dietz)	0.03 (0.09)	—	—	—	R	5	—	—	—	H	N	
<i>Pheloconus hispidus</i> (LeConte)	—	0.06 (0.18)	0.06 (0.12)	—	R	—	11	11, 12	—	H	N	
<i>Trichodirabius longulus</i> (LeConte)	—	—	0.06 (0.12)	—	R	—	—	4, 11	—	H	N	
Elateridae												
<i>Drapetes rubricollis</i> LeConte	—	—	—	0.03 (0.09)	R	—	—	—	3	H	N	
Languriidae												
<i>Loberus</i> sp.	—	0.06 (0.12)	—	—	R	—	4, 12	—	—	H	N	
Lycidae												
<i>Plateros</i> sp.	—	—	—	0.03 (0.09)	R	—	—	—	2	D/H ¹¹	N	

TABLE 1. (CONTINUED) HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Scarabaeidae												
<i>Trigonopeltastes delta</i> (Forster)	0.09 (0.27)	—	—	—	R	5	—	—	—	D/H	N	
Collembola												
Sminthuridae												
<i>Sminthurus</i> sp.	0.03 (0.09)	—	—	—	R	11	—	—	—	H		
<i>Sminthurinus</i> sp.	0.03 (0.09)	—	—	—	R	11	—	—	—	H		
Dermaptera												
Forficulidae												
poss. ¹² <i>Doru taeniatum</i> Dohrn	—	0.03 (0.09)	—	—	R	—	11	—	—	H		
Diptera												
Agromyzidae												
<i>Melangromyza</i> sp.	0.09 (0.27)	0.09 (0.19)	—	—	O	11	4, 11	—	—	H/H		
Unidentified sp.	0.03 (0.09)	0.03 (0.09)	—	—	R	12	11	—	—	H/H		
Bibionidae												
Unidentified sp.	—	—	0.03 (0.09)	—	R	—	—	3	—	H/H		
Otitidae												
<i>Chaetopsis massyla</i> (Walker)	0.03 (0.09)	0.03 (0.09)	—	—	R	12	12	—	—	H/H		
<i>Euxesta juncta</i> Coquiller	0.03 (0.09)	—	—	—	R	3	—	—	—	H/H		
Sarcophagidae												
<i>Ravinia derelicta</i> Walker	0.03 (0.09)	0.03 (0.09)	0.38 (1.06)	0.03 (0.09)	C	4	5	5	12	D/H		
Sciaridae												
Unidentified sp.	0.03 (0.09)	—	0.16 (0.30)	—	O	5	—	11, 12	—	D/H		
Syrphidae												
<i>Toxomerus boscii</i> (Macquart)	—	0.13 (0.13)	—	—	R	—	3, 6, 11, 12	—	—	P/H		
<i>Toxomerus politus</i> (Say)	—	0.09 (0.19)	0.03 (0.09)	—	R	—	11, 12	1	—	P/H		
Tephritidae												
<i>Acinia pictura</i> (Snow)	0.06 (0.12)	0.28 (0.53)	—	—	C	5, 11	1, 3, 12	—	—	H/U		
<i>Dioxya picciola</i> (Bigot)	0.69 (0.86)	0.22 (0.43)	0.22 (0.41)	0.06 (0.18)	C	1-5, 11, 12	4, 11, 12	11, 12	11, 12	H/U		
<i>Euaresta bella</i> (Loew)	—	0.03 (0.09)	—	—	R	—	11	—	—	H/U		
<i>Trupanea actinobola</i> (Loew)	0.03 (0.09)	—	0.13 (0.35)	—	O	12	—	11	—	H/U		
<i>Xanthaciura insecta</i> (Loew)	0.50 (0.97)	—	—	—	C	1, 11, 12	—	—	—	H/U		

TABLE 1. (CONTINUED) HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Therevidae												
<i>Cyclotelus picitipennis</i> (Wiedmann)	—	0.03 (0.09)	—	—	R	—	6	—	—	P/H		
Tipulidae												
Unidentified spp. (2 morphotypes)	0.06 (0.18)	—	—	—	R	11	—	—	—	D/H		
Hemiptera												
Alydidae												
<i>Hyalymenus</i> sp. A	0.03 (0.09)	0.38 (0.35)	—	—	C	4	1, 2, 4-6	—	—	H	N	
<i>Hyalymenus</i> sp. B	0.06 (0.12)	0.03 (0.09)	—	—	R	5, 11	12	—	—	H	N	
Imm. sp.	—	—	0.03 (0.09)	—	R	—	—	11	—	H		
Coreidae												
<i>Leptoglossus phyllopus</i> (L.)	0.03 (0.09)	0.09 (0.13)	—	—	R	11	1, 4, 12	—	—	H	N	*
Issidae												
<i>Acanalonia servillei</i> Spinola	0.03 (0.09)	—	—	—	R	6	—	—	—	H		
Largidae												
<i>Largus davisi</i> Barber	—	0.03 (0.09)	—	—	R	—	5	—	—	H	N	
Lygaeidae												
<i>Neortholomus koreshanus</i> (Van Duzee)	0.03 (0.09)	—	—	0.06 (0.12)	R	2	—	—	2, 12	H		
<i>Neopamera bilobata</i> (Say)	0.03 (0.09)	0.06 (0.12)	—	—	R	5	1, 12	—	—	H		*
poss. <i>Nysius</i> sp.	—	0.13 (0.27)	—	—	R	—	6, 12	—	—	H		
<i>Oedancala crassimana</i> (Fabricius)	0.41 (0.60)	0.06 (0.12)	0.25 (0.52)	—	C	5, 6, 11	3, 6	1, 4, 12	—	H		
<i>Oncopeltus fasciatus</i> (Dallas)	0.03 (0.09)	—	—	—	R	1	—	—	—	H		
<i>Paromius longulus</i> (Dallas)	0.22 (0.41)	0.13 (0.35)	0.03 (0.09)	—	C	11, 12	12	12	—	H		*
Imm. spp.	0.25 (0.44)	0.41 (0.65)	0.03 (0.09)	—	C	1, 11, 12	2, 11, 12	4	—	H		
Miridae												
<i>Creontiades</i> sp.	—	0.03 (0.09)	0.03 (0.09)	—	R	—	1	4	—	H		*
<i>Dagbertus semipictus</i> (Blatchley)	—	—	0.03 (0.09)	—	R	—	—	2	—	H		
<i>Reuteroscopus ornatus</i> (Reuter)	—	—	0.03 (0.09)	—	R	—	—	6	—	H		
<i>Taylorilygus pallidulus</i> (Blanchard)	0.06 (0.12)	0.06 (0.18)	0.13 (0.27)	—	O	1, 2	4, 11	6, 11	—	H		*
Unidentified sp. A	0.03 (0.09)	—	—	—	R	12	—	—	—			
Unidentified sp. B	0.03 (0.09)	—	—	—	R	12	—	—	—			
Pentatomidae												
<i>Loxa</i> sp.	—	0.03 (0.09)	—	—	R	—	1	—	—	H		
<i>Thyanta custator</i> (Fabricius)	—	—	0.06 (0.18)	—	R	—	—	2	—	H	N	*
<i>Thyanta perditor</i> (Fabricius)	—	0.03 (0.09)	—	—	R	—	12	—	—	H	N	*

TABLE 1. (CONTINUED) HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Rhopalidae												
<i>Liorrhysus hydlinus</i> (Fabricius)	—	—	0.03 (0.09)	—	R	—	—	11	—	H		*
Homoptera												
Aphididae												
<i>Aphis spiraeicola</i> Patch	0.13 (0.27)	0.03 (0.09)	0.03 (0.09)	—	O	1, 2	3	11	—	H	E	*
<i>Aphis</i> sp.	—	—	0.03 (0.09)	—	R	—	—	11	—	H		
<i>Eulachnus rileyi</i> (Williams)	—	—	0.03 (0.09)	—	R	—	—	1	—	H	E	
<i>Hysteronura setariae</i> (Thomas)	0.03 (0.09)	—	0.03 (0.09)	—	R	5	—	11	—	H	N	*
<i>Schizaphis</i> sp.	—	—	0.03 (0.09)	—	R	—	—	11	—	H		
<i>Tetraneura nigriabdominalis</i> (Sasaki)	—	—	0.03 (0.09)	—	R	—	—	11	—	H	E	
<i>Toxoptera aurantii</i> (Boyer de Fonscolombe)	0.06 (0.18)	0.03 (0.09)	—	—	R	11	2	—	—	H	E	*
Cercopidae												
<i>Clastoptera xantocephala</i> Germar	—	0.03 (0.09)	0.03 (0.09)	—	R	—	11	4	—	H		*
<i>Lepyronia</i> sp.	0.06 (0.12)	—	—	—	R	2, 12	—	—	—	H		
Cicadellidae												
<i>Balclutha</i> sp.	—	—	0.03 (0.09)	0.03 (0.09)	R	—	—	4	11	H		
<i>Cuerna costalis</i> (Fabricius)	—	—	0.13 (0.19)	—	R	—	—	4, 6, 12	—	H	N	
<i>Draeculacephala</i> sp. A	0.13 (0.19)	—	—	—	R	1, 11, 12	—	—	—	H		
<i>Draeculacephala</i> sp. B	—	—	0.59 (0.80)	0.03 (0.09)	C	—	—	2, 4, 11, 12	12	H		
poss. <i>Empoasca</i> sp.	0.06 (0.12)	0.13 (0.13)	—	—	O	1, 4	1, 2, 4, 12	—	—	H		
<i>Graminella nigrifrons</i> (Forbes)	—	—	0.16 (0.27)	0.03 (0.09)	O	—	—	4, 6, 12	—	H	N	
<i>Graphocephala versuta</i> (Say)	—	0.19 (0.22)	—	—	O	—	1, 4, 6, 11	—	—	H	N	
<i>Gypona</i> sp.	0.19 (0.22)	0.06 (0.18)	0.09 (0.18)	—	C	2, 4, 11, 12	2	11, 12	—	H		
<i>Homalodisca coagulata</i> (Say)	0.94 (0.74)	0.41 (0.33)	—	0.03 (0.09)	C	1-6, 11, 12	1, 4-6, 11, 12	—	11	H	N	*
<i>Hortensia similis</i> (Walker)	—	—	0.03 (0.09)	—	R	—	—	12	—	H	N	
<i>Oncometopia nigricans</i> (Walker)	0.03 (0.09)	—	—	—	R	1	—	—	—	H	N	*
<i>Paraulacizes irrorata</i> (Fabricius)	—	0.03 (0.09)	—	—	R	—	1	—	—	H		
<i>Stragania</i> sp.	0.03 (0.09)	0.09 (0.19)	0.25 (0.48)	—	C	1	11, 12	11, 12	—	H		
<i>Tropicanus costamaculatus</i> (Van Duzee)	0.06 (0.12)	—	—	—	R	3, 12	—	—	—	H		
Imm. spp.	2.19 (1.47)	1.94 (1.84)	0.72 (1.11)	0.13 (0.27)	C	1-6, 11, 12	1-6, 11, 12	3, 4, 11, 12	1, 12	H		

TABLE 1. (CONTINUED) HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Cixiidae												
<i>Bothriocera</i> sp.	—	0.19 (0.44)	—	—	O	—	5, 6	—	—	H	N	
<i>Myndus crudus</i> Van Duzee	0.03 (0.09)	0.06 (0.12)	—	—	R	11	4, 5	—	—	H	N	*
Delphacidae												
<i>Delphacodes puella</i> (Van Duzee)	—	0.06 (0.12)	—	—	R	—	1, 11	—	—	H		
<i>Delphacodes</i> sp. A	—	—	0.03 (0.09)	0.03 (0.09)	R	—	—	12	1	H		
<i>Delphacodes</i> sp. B	0.03 (0.09)	—	—	—	R	3	—	—	—	H		
Imm. sp.	—	—	0.03 (0.09)	0.03 (0.09)	R	—	—	12	12	H		
Flatidae												
Imm. sp.	0.47 (0.59)	0.03 (0.09)	—	0.16 (0.44)	C	3-6, 11	3	—	5	H		
Membracidae												
<i>Spissistilus festinus</i> (Say)	—	—	0.22 (0.53)	—	O	—	—	1, 12	—	H	N	*
<i>Stictocephala lutea</i> (Walker)	—	—	0.16 (0.19)	—	O	—	—	3, 4, 11, 12	—	H	N	
Psyllidae												
<i>Diaphorina citri</i> Kuwayama	—	—	0.03 (0.09)	—	R	—	—	3	—	H	E	*
Hymenoptera												
Agaonidae												
Unidentified sp.	0.03 (0.09)	—	—	—	R	11	—	—	—	H		
Anthophoridae												
<i>Exomalopsis</i> sp.	—	0.03 (0.09)	—	—	R	—	5	—	—	H	N	
Halictidae												
<i>Agapostemon splendens</i> (Lepeletier)	—	0.06 (0.12)	—	—	R	—	5, 12	—	—	H	N	
<i>Augochlora</i> sp.	—	0.03 (0.09)	—	—	R	—	5	—	—	H	N	
<i>Lasioglossum</i> sp.	—	—	—	0.03 (0.09)	R	—	—	—	6	H	N	
Lepidoptera												
Heliconiidae												
<i>Heliconius charitonius</i> Tuckeri	0.03 (0.09)	—	—	—	R	12	—	—	—	H		
Geometridae												
Unidentified sp. A	0.03 (0.09)	—	—	—	R	11	—	—	—	H		
Unidentified sp. B	—	—	—	0.03 (0.09)	R	—	—	—	11	H		
Unidentified sp. C	—	—	0.03 (0.09)	—	R	—	—	11	—	H		
Gracillariidae												
<i>Phyllocnistis</i> sp.	0.03 (0.09)	—	—	—	R	4	—	—	—	H		

TABLE 1. (CONTINUED) HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Noctuidae												
Unidentified sp.	—	—	—	0.03 (0.09)	R	—	—	—	12	H		
Pyralidae												
Unidentified sp. A	—	—	0.13 (0.19)	—	R	—	—	6, 11, 12	—	H		
Unidentified sp. B	—	—	0.03 (0.09)	—	R	—	—	11	—	H		
Unidentified sp. C	—	—	0.03 (0.09)	—	R	—	—	11	—	H		
Unidentified sp. D	—	—	0.03 (0.09)	—	R	—	—	11	—	H		
Unidentified sp. E	0.03 (0.09)	—	—	—	R	12	—	—	—	H		
Unidentified sp. F	—	—	0.06 (0.12)	—	R	—	—	3, 4	—	H		
Unidentified sp. G	—	0.16 (0.44)	—	—	O	—	4	—	—	H		
Unidentified sp. H	0.09 (0.27)	—	—	—	R	4	—	—	—	H		
Unidentified sp. I	—	—	0.03 (0.09)	—	R	—	—	6	—	H		
Orthoptera												
Acrididae												
<i>Leptysmia marginicollis</i> (Serville)	0.06 (0.18)	—	—	0.03 (0.09)	R	1	—	—	11	H	N	
<i>Schistocerca damnifica</i> (Saussure)	0.06 (0.12)	—	—	0.03 (0.09)	R	5, 12	—	—	4	H	N	
<i>Orphulella pelidna</i> (Burmeister)	—	—	0.03 (0.09)	—	R	—	—	6	—	H	N	
<i>Paroxya atlantica</i> Scudder	0.03 (0.09)	—	—	0.03 (0.09)	R	5	—	—	6	H	N	
Imm. spp.	0.31 (0.48)	—	0.25 (0.40)	0.50 (0.64)	C	4, 5, 6	—	3, 4, 6	2-6	H		
Gryllidae												
<i>Cyroxipha</i> poss. <i>columbiana</i> Caudell	0.03 (0.09)	—	—	0.06 (0.12)	R	1	—	—	11, 12	H	N	
<i>Oecanthus quadripunctatus</i> Beutenmuller	—	—	0.09 (0.19)	—	R	—	—	3, 12	—	H	N	
Tetrigidae												
<i>Tetrigidea lateralis</i> (Say)	—	0.03 (0.09)	—	0.03 (0.09)	R	—	12	—	11	H	N	
<i>Tetrigidea</i> sp.	—	—	0.09 (0.19)	—	R	—	—	2, 3	—	H	N	
Tettigoniidae												
<i>Conocephalus</i> sp.	—	0.53 (0.59)	0.72 (0.86)	0.03 (0.09)	C	—	1, 2, 6, 11, 12	3, 4, 6, 11, 12	12	H	N	
Imm. sp.	—	—	0.03 (0.09)	—	R	—	—	1	—	H		
Phasmatodea												
Pseudophasmatidae												
<i>Anisomorpha buprestoides</i> (Stoll)	—	—	0.22 (0.41)	0.06 (0.12)	O	—	—	2, 4	3, 4	H	N	
Psocoptera												
Peripsocidae												
<i>Peripsocus madescens</i> (Walsh)	—	—	—	1.84 (2.15)	C	—	—	—	1, 3-6	H	N	

TABLE 1. (CONTINUED) HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Psocidae												
<i>Indiopsocus ceterus</i> Mockford	—	—	—	0.03 (0.09)	R	—	—	—	4	H	N	
gen. sp.	—	—	—	0.03 (0.09)	R	—	—	—	5	H		
Thysanoptera												
Phlaeothripidae												
<i>Haplothrips gowdeyi</i> (Franklin)	—	—	0.03 (0.09)	—	R	—	—	11	—	H	N	

¹Abundance per transect for each site averaged over 8 months. Each transect equals 100 sweeps with a 90-cm diameter sweep net. One sweep consists of an 180° sweeping motion.

²Samples were taken from November (month 11) through June (month 6)..

³D = Detritivore (including scavengers), H=Herbivore (including pollen and nectar feeders), P = Predator, U = Undetermined.

⁴N = Native, E = Exotic, Blank space = Undetermined.

⁵An * indicates that the species is a known economic pest.

⁶Weston, FL, Broward Co., N26.035483 and W80.43495, *M. quinquenervia* stand under a power line.

⁷University Rd. and Griffin Rd., Fort Lauderdale, FL, Broward Co., N 26.05605 and W -80.25168, vacant lot occupied by *M. quinquenervia*.

⁸Tamiami Tr. and Corkscrew Rd., Estero, FL, Collier Co., N 26.4255 and W -81.81033, Cow pasture occupied with small *M. quinquenervia* stumps.

⁹Belle Meade, FL, Collier Co., N 26.10478 and W -81.63392, *M. quinquenervia* stand in the Picayune Forest.

¹⁰Average abundance among all sites includes total number of specimens collected. R = Rare, 1-5 specimens; O = Occasional, 6-10 specimens; C = Common, >10 specimens.

¹¹/ indicates a difference in trophic level of larvae stage and adult stage. Trophic level data include larval then adult trophic level.

¹²poss. indicates a possible identification that could not be confirmed.

TABLE 2. NON-HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Acari												
Anystidae												
<i>Anystis agilis</i> Banks	0.03 (0.09)	0.06 (0.12)	—	—	R	2	2,3	—	—	P	N	
Microtrombidiidae												
<i>Trichotrombidum muscarum</i> (Riley)	—	0.09 (0.27)	—	—	R	—	5	—	—	Pa/P ¹¹	N	
Araneae												
Anyphaenidae												
<i>Hibana</i> sp.	0.13 (0.27)	0.03 (0.09)	0.03 (0.09)	0.34 (0.52)	C	1, 4	6	12	1, 3 11, 12	P	N	
<i>Lupettiana mordax</i> (O. P.-Cambridge)	—	0.06 (0.12)	—	0.06 (0.12)	R	—	3, 11	—	2, 5	P	N	
<i>Wulfilia alba</i> (Hentz)	—	0.03 (0.09)	—	—	R	—	6	—	—	P	N	
Araneidae												
<i>Acacesia hamata</i> (Hentz)	0.47 (0.34)	0.44 (0.44)	0.06 (0.12)	0.06 (0.12)	C	2-6, 11, 12	1, 3, 6, 11, 12	6, 11	2, 11	P	N	
<i>Cyclosa turbinata</i> (Walckenaer)	0.03 (0.09)	0.13 (0.27)	—	—	O	4	5, 6	—	—	P	N	
<i>Eriophora ravilla</i> (C.L. Koch)	0.16 (0.23)	0.03 (0.09)	—	0.03 (0.09)	O	5, 6, 11	3	—	11	P	N	
<i>Gasteracantha cancriformis</i> (L.)	—	0.03 (0.09)	—	—	R	—	1	—	—	P	N	
<i>Kaira alba</i> (Hentz)	—	0.03 (0.09)	—	—	R	—	3	—	—	P	N	
<i>Mangora spiculata</i> (Hentz)	—	—	—	0.06 (0.18)	R	—	—	—	12	P	N	
<i>Mangora</i> imm. sp.	—	—	—	0.03 (0.09)	R	—	—	—	6	P	N	
<i>Neoscona arabesca</i> (Walckenaer)	0.19 (0.18)	—	—	—	O	1, 3-6	—	—	—	P	N	
<i>Neoscona</i> imm. sp.	0.97 (1.26)	0.47 (0.77)	0.09 (0.19)	—	C	1-4, 11, 12	1-3, 11	1, 4	—	P	N	
<i>Wagneriana tauricornis</i> (O. P.-Cambridge)	—	—	0.06 (0.18)	0.03 (0.09)	R	—	—	4	12	P	N	
Imm. spp.	0.66 (0.63)	0.06 (0.12)	0.03 (0.09)	0.13 (0.13)	C	1, 2, 4, 6, 11, 12	3, 6	4	1, 6, 11, 12	P	N	
Clubionidae												
<i>Clubiona</i> sp.	—	0.19 (0.44)	—	0.16 (0.35)	C	—	5, 11	—	11, 12	P	N	
Corinnidae												
<i>Castianeira</i> sp.	0.03 (0.09)	—	—	—	R	5	—	—	—	P	N	
<i>Trachelas volutus</i> Gertsch	0.06 (0.12)	—	—	—	R	5, 12	—	—	—	P	N	
Linyphiidae												
<i>Eperigone bryantae</i> Ivie & Barrows	—	—	0.03 (0.09)	—	R	—	—	12	—	P	N	
<i>Meioneta</i> sp.	0.03 (0.09)	—	0.03 (0.09)	—	R	1	—	3	—	P	N	
Unidentified sp. A	0.13 (0.27)	—	—	—	R	1, 11	—	—	—	P	N	

TABLE 2. (CONTINUED) NON-HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Lycosidae												
<i>Pardosa littoralis</i> Banks	—	—	0.06 (0.18)	—	R	—	—	12	—	P	N	
<i>Pardosa</i> imm. sp.	0.03 (0.09)	—	0.50 (1.41)	—	C	11	—	12	—	P	N	
<i>Pirata</i> sp.	0.56 (1.12)	0.06 (0.12)	0.84 (2.39)	0.69 (1.56)	C	1, 11	3, 12	12	1, 11, 12	P	N	
Mimetidae												
<i>Mimetus</i> sp.	0.03 (0.09)	—	0.06 (0.18)	0.50 (0.53)	C	3	—	12	1-4, 11	P	N	
Miturgidae												
<i>Cheiracanthium inclusum</i> (Hentz)	3.00 (2.10)	4.38 (4.89)	0.31 (0.35)	0.50 (0.44)	C	1-6, 12	1-6, 12	1, 2, 4, 6, 12	3, 5, 6, 11, 12	P	N	
Oxyopidae												
<i>Peucetia viridans</i> (Hentz)	4.28 (2.87)	0.28 (0.39)	0.34 (0.42)	0.13 (0.13)	C	1-6, 12	1, 3, 5, 12	2-4, 6, 12	1, 2, 6, 12	P	N	
Pisauridae												
<i>Pisaurina mira</i> (Walckenaer)	—	—	—	0.03 (0.09)	R	—	—	—	6	P	N	
<i>Pisaurina undulata</i> (Keyserling)	0.03 (0.09)	—	—	—	R	6	—	—	—	P	N	
<i>Pisaurina</i> imm. spp.	0.41 (0.77)	0.16 (0.27)	—	0.06 (0.12)	C	1, 2, 5, 11	1, 4, 11	—	1, 4	P	N	
Imm. sp.	0.09 (0.19)	0.03 (0.09)	—	—	R	1, 12	2	—	—	P	N	
Salticidae												
<i>Eris flava</i> (Peckham & Peckham)	0.13 (0.23)	0.16 (0.30)	0.50 (0.92)	0.28 (0.62)	C	2, 12	2, 12	1, 11, 12	1, 12	P	N	
<i>Eris</i> imm. sp.	0.03 (0.09)	0.03 (0.09)	—	—	R	11	12	—	—	P	N	
<i>Habronattus</i> sp.	—	0.03 (0.09)	0.06 (0.12)	—	R	—	2	12, 4	—	P	N	
<i>Hentzia palmarum</i> (Hentz)	2.25 (0.90)	1.41 (0.57)	0.31 (0.42)	1.72 (1.86)	C	1-6, 11, 12	1-6, 11, 12	1, 3, 6, 11, 12	1, 2, 4-6, 11, 12	P	N	
<i>Lyssomanes viridis</i> (Walckenaer)	—	0.13 (0.19)	—	—	R	—	3-5	—	—	P	N	
<i>Pelegrina galathea</i> (Walckenaer)	0.38 (0.48)	0.16 (0.19)	0.44 (0.37)	—	C	1-4, 11, 12	12, 1, 2, 6	1-4, 11, 12	—	P	N	
<i>Pelegrina</i> sp.	—	—	—	0.03 (0.09)	R	—	—	—	5	P	N	
<i>Phidippus clarus</i> Keyserling	—	—	0.06 (0.18)	—	R	—	—	4	—	P	N	
<i>Phidippus regius</i> C.L. Koch	—	—	0.03 (0.09)	—	R	—	—	12	—	P	N	
<i>Phidippus</i> sp.	—	0.03 (0.09)	—	0.16 (0.35)	O	—	5	—	12, 5	P	N	
<i>Thiodina peurpera</i> (Hentz)	—	0.59 (1.68)	—	—	C	—	6	—	—	P	N	
<i>Zygoballus sexpunctatus</i> (Hentz)	—	—	0.03 (0.09)	—	R	—	—	4	—	P	N	
<i>Zygoballus</i> sp.	—	—	—	0.03 (0.09)	R	—	—	—	2	P	N	

TABLE 2. (CONTINUED) NON-HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Tetragnathidae												
<i>Glenognatna foxi</i> (McCook)	—	—	0.13 (0.35)	—	R	—	—	12	—	P	N	
<i>Glenognatha</i> sp.	—	—	—	0.06 (0.18)	R	—	—	—	11	P	N	
<i>Leucauge argyra</i> (Walckenaer)	—	0.03 (0.09)	—	—	R	—	12	—	—	P	N	
<i>Tetragnatha</i> sp.	1.19 (0.61)	0.28 (0.28)	0.16 (0.35)	0.03 (0.09)	C	1-6, 11, 12	12, 2-4, 6	11, 12	11	P	N	
Theridiidae												
<i>Anelosimus studiosus</i> (Hentz)	2.09 (1.41)	—	0.09 (0.27)	—	C	1-6, 11, 12	—	12	—	P	N	
<i>Chrysso pulcherrima</i> (Mello-Leitao)	0.03 (0.09)	—	0.03 (0.09)	0.13 (0.35)	O	11	—	11	11	P	N	
<i>Dipoena nigra</i> (Emerton)	—	—	—	0.03 (0.09)	R	—	—	—	5	P	N	
<i>Latrodectus geometricus</i> C.L. Koch	—	—	0.03 (0.09)	—	R	—	—	4	—	P	N	
<i>Theridion flavonotatum</i> Becker	0.75 (0.69)	—	—	0.06 (0.12)	C	11, 1-3, 3, 5, 6	—	—	11, 2	P	N	
<i>Theridion glaucescens</i> Becker	0.38 (0.57)	—	—	0.03 (0.09)	C	11, 3, 4	—	—	11	P	N	
<i>Theridion</i> imm. sp.	0.13 (0.27)	0.03 (0.09)	0.03 (0.09)	—	O	2, 5	5	2	—	P	N	
<i>Thymoites</i> sp.	0.06 (0.18)	—	—	—	R	12	—	—	—	P	N	
Thomisidae												
<i>Misumenoides formosipes</i> (Walckenaer)	—	0.03 (0.09)	—	—	R	—	11	—	—	P	N	
<i>Misumenops bellulus</i> (Banks)	0.81 (0.53)	1.16 (1.14)	0.84 (0.67)	0.47 (0.39)	C	1-5, 11, 12	1-6, 11, 12	1-4, 6, 11, 12	11, 1, 2, 4-6	P	N	
<i>Misumenops oblongus</i> (Keyserling)	—	—	0.06 (0.18)	0.03 (0.09)	R	—	—	4	1	P	N	
<i>Misumenops</i> imm. spp.	0.50 (0.40)	0.13 (0.19)	1.09 (1.13)	0.19 (0.44)	C	1-4, 6, 11, 12	2, 11, 12	1-4, 11, 12	5, 11	P	N	
<i>Tmarus</i> sp.	0.06 (0.12)	—	0.03 (0.09)	1.63 (0.86)	C	11, 6	—	1	1-6, 11, 12	P	N	
Coleoptera												
Coccinellidae												
<i>Brachiacantha decora</i> Casey	—	0.06 (0.18)	—	—	R	—	6	—	—	P	N	
<i>Coelophora inaequalis</i> (Fabricius)	—	0.03 (0.09)	—	—	R	—	12	—	—	P	N	
<i>Cycloneda sanguinea</i> (L.)	0.03 (0.09)	0.06 (0.12)	0.09 (0.13)	—	O	12	1, 3	1, 3, 6, 11	—	P	N	
<i>Exochomus marginipennis</i> (LeConte)	—	—	0.06 (0.12)	—	R	—	—	11, 12	—	P	N	
<i>Psyllobora parvnotata</i> Casey	0.03 (0.09)	0.03 (0.09)	—	—	R	3	12	—	—	P	N	
<i>Scymnus securus</i> J. Chapin	—	—	0.03 (0.09)	—	R	—	—	12	—	P	N	
<i>Scymnus</i> sp.	0.03 (0.09)	0.09 (0.13)	—	—	R	4	2, 3, 5	—	—	P	N	

TABLE 2. (CONTINUED) NON-HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Lampyridae												
<i>Pyropyga minuta</i> LeConte	0.03 (0.09)	—	—	—	R	3	—	—	—	P	N	
Scirtidae												
<i>Cyphon</i> sp.	0.25 (0.53)	—	—	—	O	4, 6	—	—	—	D	N	
Diplopoda												
Spirobolidae												
<i>Chicobolus spinigerus</i> (Wood)	0.06 (0.18)	—	—	—	R	12	—	—	—	D	N	
Dictyoptera												
Blattellidae												
<i>Choristoneura parishii</i> Rehn	0.19 (0.22)	0.28 (0.60)	—	—	C	1, 5, 11, 12	3, 5, 12	—	—	D	E	
Imm. sp.	—	—	0.03 (0.09)	—	R	—	—	2	—			
Mantidae										D		
<i>Gonatista grisea</i> (Fabricius)	—	0.06 (0.12)	—	—	R	—	11, 12	—	—	P	N	
<i>Stagmomantis</i> sp.	0.03 (0.09)	—	—	—	R	6	—	—	—	P	N	
<i>Thesprotia graminis</i> (Scudder)	—	0.03 (0.09)	—	—	R	—	12	—	—	P	N	
Imm. spp.	—	0.09 (0.19)	—	0.16 (0.30)	O	—	5, 12	—	3, 4	P		
Diptera												
Ceratopogonidae												
<i>Atrichopogon</i> sp.	0.06 (0.12)	0.63 (1.13)	—	0.03 (0.09)	C	2, 11	1, 11, 12	—	12	D/Pa		
Unidentified sp. A	0.03 (0.09)	0.25 (0.48)	0.38 (1.06)	—	C	2	1, 11	11	—	D/Pa		
Unidentified sp. B	—	0.03 (0.09)	—	0.50 (1.41)	C	—	11	—	11	D/Pa		
Unidentified sp. C	—	—	—	0.03 (0.09)	R	—	—	—	1	D/Pa		
Chironomidae												
Unidentified spp. (11 morphotypes)	0.53 (0.36)	1.28 (2.07)	0.84 (1.08)	0.03 (0.09)	C	1, 2, 4-6, 11, 12	1, 2, 11, 12	1, 3, 4, 11, 12	11	U/U		
Chloropidae												
<i>Apallates dissidens</i> Tucker	—	0.13 (0.19)	0.34 (0.97)	0.06 (0.18)	C	—	1, 11, 12	11	12	U/U		
<i>Apallates neocoxendrix</i> Sabrosky	0.03 (0.09)	0.06 (0.18)	—	0.19 (0.53)	O	5	1	—	11	U/U		
<i>Coniscinella</i> sp.	0.19 (0.29)	0.03 (0.09)	0.03 (0.09)	0.06 (0.08)	C	1, 2, 11	2	4	11	U/U		
<i>Chlorops</i> sp.	—	—	0.22 (0.41)	—	O	—	—	4, 11	—	U/U		
<i>Ectecephala unicolor</i> (Loew)	—	0.03 (0.09)	—	—	R	—	1	—	—	U/U		
<i>Hippelates plebejus</i> Loew	—	—	0.06 (0.18)	—	R	—	—	6	—	D/Pa		
<i>Liohippelates pusio</i> Loew	—	0.03 (0.09)	0.59 (1.29)	—	C	—	3	1, 3, 6, 11	—	U/U		

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Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Unidentified sp. A	0.03 (0.09)	—	—	—	R	12	—	—	—	U/U		
Unidentified sp. B	0.06 (0.18)	—	—	—	R	1	—	—	—	U/U		
Unidentified sp. C	0.03 (0.09)	0.03 (0.09)	—	—	R	12	1	—	—	U/U		
Unidentified sp. D	—	0.06 (0.18)	—	—	R	—	1	—	—	U/U		
Unidentified sp. E	—	0.03 (0.09)	—	—	R	—	6	—	—	U/U		
Clusiidae												
Unidentified sp.	—	0.03 (0.09)	—	—	R	—	12	—	—	D/U		
Culicidae												
Unidentified spp. (2 morphotypes)	—	—	—	0.13 (0.23)	R	—	—	—	6, 11	D/Pa		
Dolichopodidae												
<i>Chrysotus</i> sp.	1.34 (1.56)	1.69 (1.99)	0.72 (1.47)	0.06 (0.12)	C	1-6, 11	1-6, 11	4, 11, 12	4, 11	P/P		
<i>Chrysotus picticornis</i> Loew	0.13 (0.35)	—	0.22 (0.62)	—	C	5	—	11	—	P/P		
<i>Condylostylus</i> sp.	0.03 (0.09)	—	0.03 (0.09)	—	R	5	—	11	—	P/P		
<i>Condylostylus tonsus</i> Aldrich	—	0.38 (0.46)	0.16 (0.44)	—	C	—	2, 4, 12	4	—	P/P		
Empididae												
<i>Euhybus</i> poss. <i>stramaticus</i> Melander	0.13 (0.27)	0.09 (0.19)	—	0.03 (0.09)	O	2, 5	2, 3	—	4	P/P		
<i>Euhybus</i> sp.	0.03 (0.09)	—	—	—	R	6	—	—	—	P/P		
<i>Syneches simplex</i> Walker	—	0.06 (0.12)	0.03 (0.09)	0.06 (0.18)	O	—	1, 12	12	12	P/P		
Unidentified sp.	—	0.03 (0.09)	—	—	R	—	4	—	—	P/P		
Ephydriidae												
Unidentified sp. A	—	0.09 (0.19)	—	—	R	—	11, 12	—	—	U/U		
Unidentified sp. B	—	0.03 (0.09)	0.09 (0.27)	0.03 (0.09)	O	—	11	11	12	U/U		
Unidentified sp. C	—	—	0.06 (0.18)	—	R	—	—	3, 11	—	U/U		
Unidentified sp. D	0.03 (0.09)	—	—	—	R	3	—	—	—	U/U		
Unidentified sp. E	0.13 (0.27)	—	—	—	R	3, 5	—	—	—	U/U		
Lauxaniidae												
Unidentified sp. A	0.03 (0.09)	0.16 (0.30)	—	—	O	2	1, 2	—	—	D/U		
Unidentified sp. B	—	—	0.03 (0.09)	—	R	—	—	6	—	D/U		
Milichiidae												
<i>Desmometopa</i> sp.	—	0.06 (0.18)	—	—	R	—	2	—	—	D/U		
Muscidae												
<i>Stomoxys calcitrans</i> (L.)	—	—	0.03 (0.09)	—	R	—	—	6	—	Pa/D		
Unidentified spp. (8 morphotypes)	0.13 (0.27)	0.28 (0.28)	0.59 (0.86)	0.19 (0.44)	C	4, 5	1, 2, 4, 5, 12	3, 4, 6, 11, 12	11, 12	U/U		

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Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Otitidae												
<i>Herina narytia</i> (Walker)	2.00 (1.57)	—	—	—	C	1-6, 11, 12	—	—	—	U/U		
Sciomyzidae												
<i>Dictya</i> sp.	0.03 (0.09)	—	—	—	R	4	—	—	—	U/U		
Sepsidae												
<i>Palaeosepsis insularis</i> (Williston)	—	0.03 (0.09)	0.03 (0.09)	—	R	—	11	11	—	D/U		
Stratiomyidae												
<i>Nemotelus glaber</i> Loew	0.13 (0.23)	—	—	—	R	4, 5	—	—	—	U/U		
Tabanidae												
<i>Chrysops</i> sp.	0.06 (0.18)	—	0.03 (0.09)	—	R	4	—	6	—	D/Pa		
Hemiptera												
Pentatomidae												
<i>Euthyrhynchus floridanus</i> (Pointer)	0.03 (0.09)	—	—	—	R	4	—	—	—	P	N	
<i>Podisus mucronatus</i> Uhler	0.19 (0.18)	0.03 (0.09)	3.06 (5.29)	0.13 (0.35)	C	2, 3, 5, 11, 12	2	1, 3, 4, 11, 12	12	P	N	
<i>Podisus sagitta</i> (Fabricius)	0.06 (0.18)	0.03 (0.09)	—	—	R	11	5	—	—	P	N	
<i>Sphyrocoris obliquus</i> (Germar)	0.03 (0.09)	0.13 (0.27)	—	—	O	12	11, 12	—	—	P	N	
<i>Stiretrus anchorago</i> (Fabricius)	0.03 (0.09)	—	0.03 (0.09)	—	R	11	—	1	—			
Imm. spp.	—	—	0.09 (0.27)	—	R	—	—	4	—	P		
Phymatidae												
Unidentified sp.	0.03 (0.09)	—	—	—	R	11	—	—	—	P		
Reduviidae												
<i>Zelus longipes</i> (L.)	0.78 (0.73)	—	—	0.03 (0.09)	C	1-3, 5, 6, 11, 12	—	—	—	P	N	
Homoptera												
Derbidae												
<i>Cedusa</i> sp.	0.13 (0.19)	1.22 (1.28)	—	—	C	3, 11, 12	2-6, 11, 12	—	—	D		
Hymenoptera												
Aphidiidae												
<i>Lysiphebus testaceipes</i> (Cresson)	—	—	0.03 (0.09)	—	R	—	—	11	—	Pa		
Braconidae												
<i>Apanteles</i> sp.	0.06 (0.18)	—	0.03 (0.09)	—	R	1	—	3	—	Pa	N	
<i>Bassus</i> sp.	—	0.03 (0.09)	0.03 (0.09)	—	R	—	11	11	—	Pa	N	

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Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
<i>Cotesia</i> sp.	—	0.06 (0.12)	—	—	R	—	3, 11	—	—	Pa	N	
Unidentified sp. A	—	—	0.06 (0.12)	—	R	—	—	3, 12	—	Pa		
Unidentified sp. B	0.03 (0.09)	—	—	—	R	12	—	—	—	Pa		
Unidentified sp. C	—	0.03 (0.09)	—	—	R	—	—	12	—	Pa		
Unidentified sp. D	—	0.03 (0.09)	—	—	R	—	3	—	—	Pa		
Unidentified sp. E	—	0.03 (0.09)	—	—	R	—	6	—	—	Pa		
Bethylidae												
Unidentified sp. A	—	—	0.03 (0.09)	—	R	—	—	12	—	Pa		
Chrysididae												
<i>Chrysis</i> sp.	0.03 (0.09)	0.13 (0.23)	—	—	O	2	5, 12	—	—	Pa	N	
Encyrtidae												
poss. <i>Aenasioidea</i> sp.	0.03 (0.09)	—	—	—	R	3	—	—	—	Pa		
<i>Anagyrus</i> sp. A	0.03 (0.09)	0.03 (0.09)	—	—	R	4	3	—	—	Pa		
<i>Anagyrus</i> sp. B	0.03 (0.09)	—	—	—	R	11	—	—	—	Pa		
poss. <i>Cercobelus</i> sp.	0.03 (0.09)	—	—	—	R	1	—	—	—	Pa		
poss. <i>Syrphophagus</i> sp.	—	—	0.03 (0.09)	—	R	—	—	12	—	Pa		
Eucoilidae												
<i>Eucoila</i> sp.	—	0.03 (0.09)	—	—	R	—	1	—	—	Pa		
Unidentified sp.	—	—	0.03 (0.09)	—	R	—	—	11	—	Pa		
Eulophidae												
<i>Cirrospilus</i> poss. <i>pictus</i> (Nees)	—	0.03 (0.09)	—	—	R	—	1	—	—	Pa	E	
Unidentified sp.	0.03 (0.09)	0.03 (0.09)	—	—	R	11	11	—	—	Pa		
Eumenidae												
<i>Zethus slossonae</i> (Zethusculus)	0.03 (0.09)	—	—	—	R	12	—	—	—	P	N	
Eupelmidae												
<i>Anastatus</i> sp.	—	0.03 (0.09)	—	—	R	—	12	—	—	Pa		
<i>Eupelmus</i> sp.	—	0.03 (0.09)	—	—	R	—	1	—	—	Pa		
Eurytomidae												
<i>Eurytoma</i> sp.	—	0.03 (0.09)	—	—	R	—	6	—	—	Pa		
Formicidae												
<i>Brachymyrmex obscurior</i> Forel	0.09 (0.13)	0.03 (0.09)	—	—	R	1, 5, 11	5	—	—	P		
<i>Camponotus floridanus</i> (Buckley)	0.44 (0.55)	—	—	0.06 (0.12)	C	3, 5, 6, 11, 12	—	—	1, 5	P	N	
<i>Camponotus planatus</i> Roger	2.34 (1.08)	1.44 (1.23)	0.06 (0.12)	—	C	1-6, 11, 12	1-6, 11, 12	12, 3	—	P	E	

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Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
<i>Camponotus sexguttatus</i> (Fabricius)	0.03 (0.09)	—	—	—	R	5	—	—	—	P	E	
<i>Cardiocondyla wroughtoni</i> obscurior Wheeler	0.03 (0.09)	—	—	—	R	11	—	—	—	P	E	
<i>Crematogaster ashmeadi</i> Mayr	—	—	0.03 (0.09)	—	R	—	—	12	—	P	N	
<i>Crematogaster atkinsoni</i> Wheeler	0.06 (0.12)	—	—	—	R	1, 11	—	—	—	P	N	
<i>Cyphomyrmex rimosus</i> (Spinola)	—	—	0.03 (0.09)	—	R	—	—	4	—	P	E	
<i>Dolichoderus pustulatus</i> Mayr	0.19 (0.44)	—	—	—	O	6, 12	—	—	—	P	N	
<i>Dorymyrmex bureni</i> (Trager)	—	0.03 (0.09)	—	—	R	—	2	—	—	P	N	
<i>Gnamptogenys aculeaticoxae</i> (Santschi)	0.03 (0.09)	—	—	—	R	5	—	—	—	P	E	
<i>Odontomachus ruginodus</i> Smith	0.03 (0.09)	—	—	—	R	11	—	—	—	P	E	
<i>Paratrechina guatemalensis</i> (Forel)	0.50 (0.94)	0.06 (0.18)	—	0.19 (0.53)	C	3, 4, 11, 12	1	—	12	P	E	
<i>Paratrechina longicornis</i> (Latreille)	2.66 (4.86)	3.19 (5.37)	—	0.13 (0.27)	C	1-4, 11, 12	3, 5, 6, 11, 12	—	2, 11	P	E	
<i>Platythyrea punctata</i> (Smith)	0.03 (0.09)	—	—	—	R	12	—	—	—	P		
<i>Pseudomyrmex ejectus</i> (Smith)	0.03 (0.09)	0.03 (0.09)	—	—	R	5	6	—	—	P	N	
<i>Pseudomyrmex gracilis</i> (Fabricius)	0.06 (0.12)	0.03 (0.09)	—	0.19 (0.22)	O	4, 6	4	—	3, 4, 6, 11	P	E	
<i>Pseudomyrmex pallidus</i> (Smith)	0.47 (0.49)	0.34 (0.68)	—	—	C	1, 2, 4, 6, 11, 12	1, 3, 4, 11	—	—	P	N	
<i>Solenopsis invicta</i> Buren	0.41 (0.58)	0.50 (0.33)	0.50 (0.61)	2.00 (4.55)	C	1, 2, 4, 11, 12	1-4, 6, 11, 12	2, 4, 6, 11, 12	2, 11	P	E	*
<i>Technomyrmex albipes</i> (Smith)	—	—	0.03 (0.09)	—	R	—	—	12	—	P	E	
Ichneumonidae												
<i>Diadegma</i> sp.	—	—	0.03 (0.09)	—	R	—	—	1	—	Pa		
Megaspilinidae												
<i>Dendrocerus</i> sp.	0.03 (0.09)	—	—	—	R	2	—	—	—	Pa		
Mutillidae												
<i>Dasymutilla</i> sp.	0.03 (0.09)	—	—	—	R	11	—	—	—	Pa	N	
Mymaridae												
<i>Anaphes</i> sp.	—	0.06 (0.12)	—	—	R	—	1, 11	—	—	Pa		
Pteromalidae												
<i>Pachyneuron</i> sp.	0.03 (0.09)	—	—	—	R	11	—	—	—	Pa		
poss. <i>Pteromalus</i> sp.	—	0.03 (0.09)	—	—	R	—	3	—	—	Pa		
Unidentified sp. A	0.03 (0.09)	—	—	—	R	11	—	—	—	Pa		
Unidentified sp. B	0.03 (0.09)	—	—	—	R	3	—	—	—	Pa		

TABLE 2. (CONTINUED) NON-HERBIVOROUS ARTHROPODS COLLECTED IN THE ABOVE-GROUND PORTIONS OF THE INVASIVE TREE, *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA, USA.

Species	Abundance per site ¹					Months collected ²				Trophic ³ level	Native/ ⁴ Exotic	Pest ⁵ status
	A ⁶	B ⁷	C ⁸	D ⁹	Ave. ¹⁰	A	B	C	D			
Scelionidae												
<i>Macroteleia</i> sp.	—	—	0.03 (0.09)	—	R	—	—	12	—	Pa		
<i>Telenomus</i> sp.	—	0.06 (0.12)	0.03 (0.09)	—	R	—	1, 11	12	—	Pa		
<i>Trissolcus</i> sp.	—	0.25 (0.33)	—	—	O	—	1, 2, 5, 12	—	—	Pa		
Sphecidae												
<i>Tachytes</i> sp.	—	—	0.03 (0.09)	—	R	—	—	11	—	Pa		
Torymidae												
<i>Torymus</i> sp.	—	0.09 (0.19)	—	—	R	—	3, 12	—	—	Pa		
Vespidae												
<i>Mischocyttarus mexicanus</i> (Saussure)	—	0.09 (0.13)	—	—	R	—	2, 4, 5	—	—	P	N	
<i>Polistes dorsalis</i> (Fabricius)	—	0.09 (0.19)	—	—	R	—	11, 12	—	—	P	N	
<i>Polistes major</i> Beauvios	—	0.03 (0.09)	—	—	R	—	1	—	—	P	N	
Neuroptera												
Chrysopidae												
<i>Ceraeochrysa</i> sp.	—	0.03 (0.09)	—	0.13 (0.23)	O	—	1	—	11, 12	P		
<i>Chrysopa quadripunctatus</i> Burmeister	—	—	—	0.03 (0.09)	R	—	—	—	11	P		
<i>Chrysoperia</i> sp.	0.06 (0.18)	0.06 (0.12)	—	—	R	1	1, 5	—	—	P		
Odonata												
Coenagrionidae												
<i>Ischnura hastata</i> (Say)	0.03 (0.09)	—	0.03 (0.09)	0.06 (0.12)	R	3	—	11	11, 12	P	N	
<i>Nehalennia pallidula</i> Calvert	0.03 (0.09)	—	—	—	R	5	—	—	—	P	N	
Libellulidae												
<i>Erythrodiplax minusula</i> (Rambus)	—	—	—	0.03 (0.09)	R	—	—	—	11	P	N	
Thysanoptera												
Phlaeothripidae												
<i>Nesothrips lativentris</i> (Karny)	—	0.16 (0.44)	—	—	O	—	12	—	—	D	N	

¹Abundance per transect for each site averaged over 8 months. Each transect equals 100 sweeps with a 90cm diameter sweep net. One sweep consists of an 180° sweeping motion.

²Samples were taken from November (month 11) through June (month 6).

³D = Detritivore (including scavengers), Pa = Parasitoid (including secretion feeders and blood suckers), P = Predator, U = Undetermined.

⁴N = Native, E = Exotic, Blank space = Undetermined.

⁵An * indicates that the species is a known economic pest.

⁶Weston, FL, Broward Co., N 26.035483 and W -80.43495, *M. quinquenervia* stand under a power line.

⁷University Rd. and Griffin Rd., Fort Lauderdale, FL, Broward Co., N 26.05605 and W -80.25168, vacant lot occupied by *M. quinquenervia*.

⁸Tamiami Tr. and Corkscrew Rd., Estero, FL, Collier Co., N 26.4255 W -81.81033, Cow pasture occupied with small *M. quinquenervia* stumps.

⁹Belle Meade, FL, Collier Co., N 26.10478 W -81.63392, *M. quinquenervia* stand in the Picayune Forest.

¹⁰Average abundance among all sites includes total number of specimens collected. R = Rare, 1-5 specimens; O = Occasional, 6-10 specimens; C = Common, >10 specimens.

¹¹/ indicates a difference in trophic level of larvae stage and adult stage. Trophic level data include larval then adult trophic level.

city of herbivores indicates that direct competition between natives and introduced biological control agents will be minimal.

Habitats dominated by invasive plants are often assumed to be sterile environments with few wildlife species utilizing the ecosystem (Bodle et al. 1994). However, Mazzotti et al. (1981) determined that differences exist among invasive plants in their ability to support native fauna, indicating that habitats invaded and dominated by non-indigenous plants are not necessarily biological deserts. After eight months of surveying arthropods in melaleuca dominated ecosystems, rarefaction curves of both herbivorous and non-herbivorous arthropods suggests that continued surveying efforts would result in the collection of additional species (Figs. 1 and 2; Magurran 1988). The variety of arthropods, both collected (Tables 1 and 2) and predicted (Figs. 1 and 2), reported herein indicates that melaleuca dominated habitats do support an arthropod community. However, this does not necessarily imply that melaleuca is a superior habitat for such fauna as indicated by the paucity of basal trophic levels (i.e., herbivores). Without the ability to compare arthropod diversity in surrounding native habitats, the probability that many species are tran-

sient, and considering the dearth of commonly collected arthropods, caution should be exercised when making conclusions concerning the functional well being of melaleuca invaded ecosystems.

The role of invasive species as facilitators of other invasive species has received little attention in the literature (Simberloff & Von Holle 1999). One example of this interaction may include the ability of nonindigenous plants to modify the habitat in a way that favors exotics over natives. In this study, 20 exotic species were collected in the melaleuca habitat (Tables 1 and 2). Among the exotic species, *Solenopsis invicta* Buren, the red imported fire ant, was common (Table 2) and is included as one of the most ecologically destructive invasive species in the southeastern U.S. These ant colonies not only cause human disturbance, but also are known to cause 70% mortality of freshwater turtle hatchlings (*Pseudemys nelsoni* Carr), can negatively impact the endangered Schaus swallowtail (*Papilio aristodemus porceanus*), and can dramatically change arthropod communities (Porter et al. 1988; Allen et al. 2001; Forsys et al. 2001). Although native to Florida, the glassy-winged sharpshooter is an invasive species in California, where it vectors *Xylella fastidiosa* Wells et al., the causal agent of Pierce's disease in vineyards. Because the

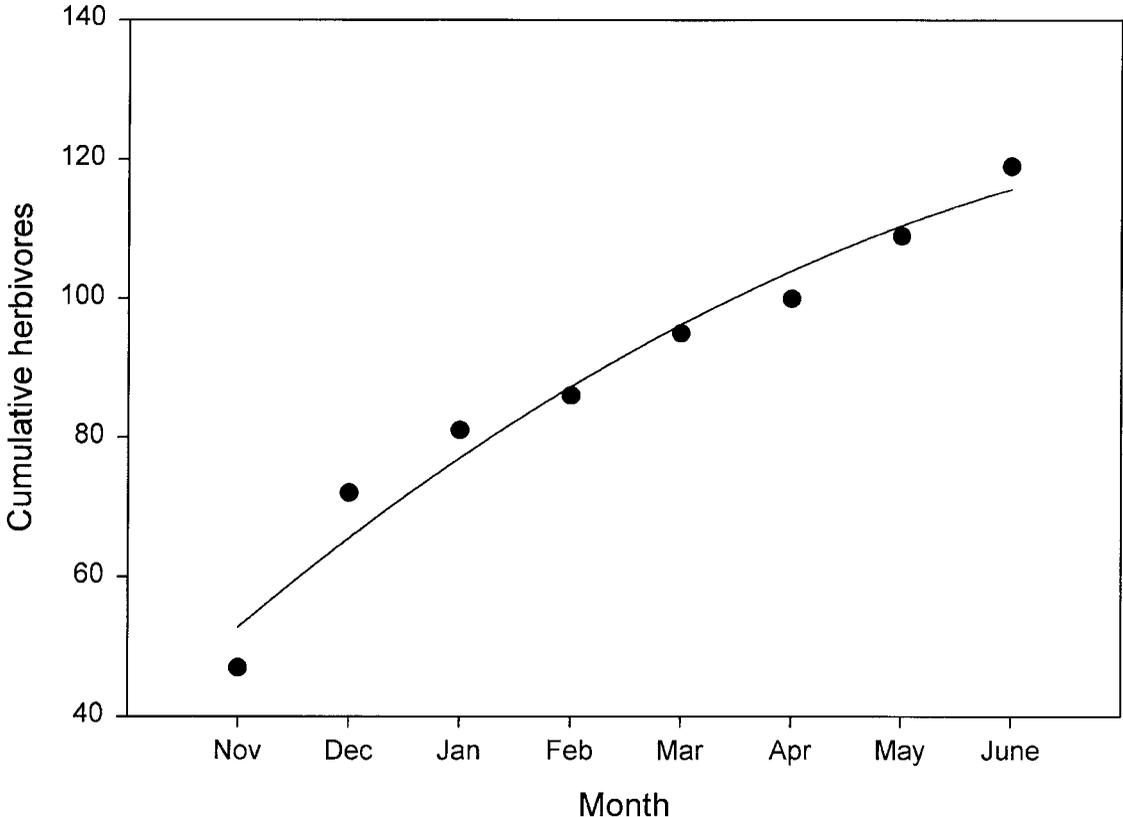


Fig. 1. Rarefaction curve for cumulative herbivorous species collected from *M. quinquenervia* (Nov.-June).

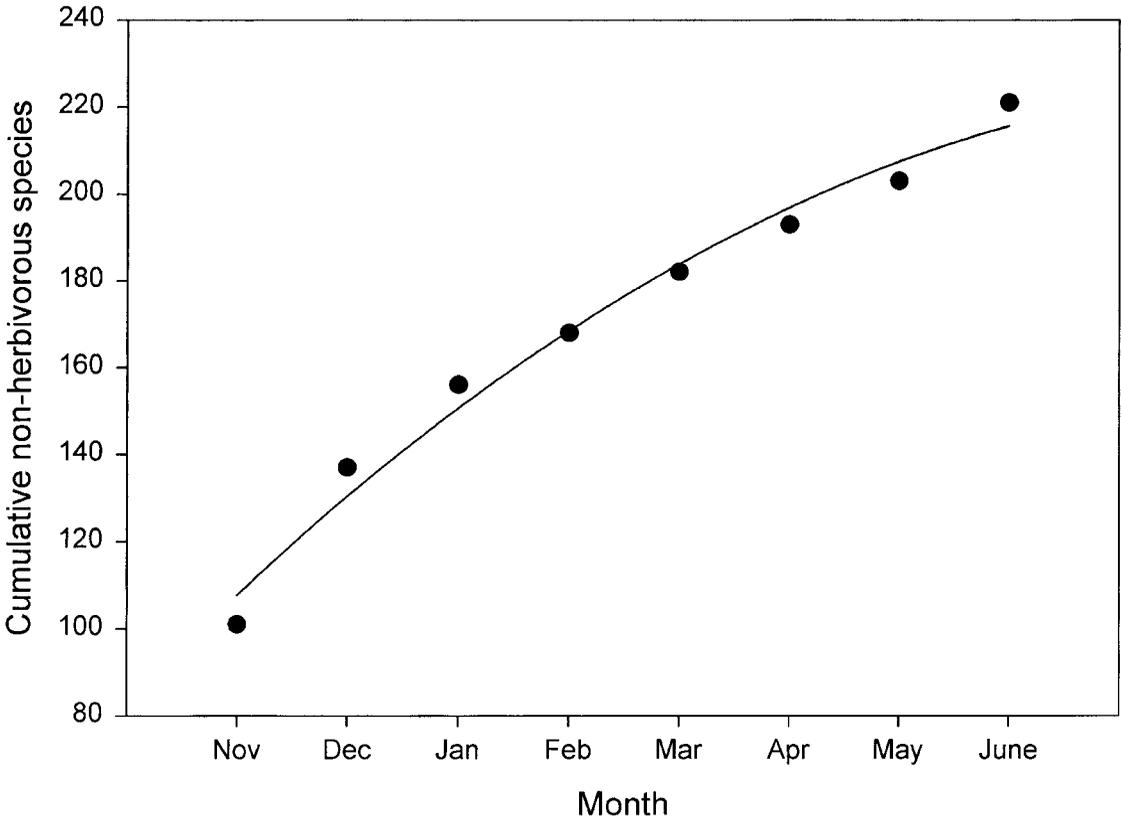


Fig. 2. Rarefaction curve for cumulative non-herbivorous species collected from *M. quinquenervia* (Nov.-June).

glassy-winged sharpshooter is commonly associated with melaleuca in Florida, it may be predicted that the plant also provides a refuge for the invasive sharpshooter in California. In this manner, melaleuca may serve as a reservoir for these and other invasive species in Florida and beyond.

In addition to the facilitation of ecological impacts by exotic species, invasive weeds may also harbor agricultural pests. For instance, 1/3 of the phytophagous insects associated with *Salsola kali* L. var. *tenuifolia* Tausch (Russian thistle) and 1/2 of the insect species on *Carduus pycnocephalus* L. (Italian thistle) proved to be pests of agricultural importance (Goeden & Ricker 1968). In our study, 18 arthropods collected from melaleuca canopies are major or minor economic pests of agricultural crops. Three species, *Aphis spiraeicola* Patch (Aphididae), *T. aurantii* (Aphididae), and *S. invicta* (Formicidae), were commonly associated with melaleuca. Both aphid species are cosmopolitan, phytophagous pests of *Citrus* spp. and many other plants. An infestation of these aphid species can result in abortion of *Citrus* flower buds and both aphids produce honeydew, thus favoring the development of sooty molds.

Native predators, parasitoids, and pathogens have interfered with half of the published case

histories involving insect introductions for weed control (Goeden & Louda 1976). Parasitoids and pathogens, for instance, caused 24% larval mortality of the introduced moth, *Samea multiplicalis* Guenee (Semple & Forno 1987). Herein, we collected several generalist predators that may potentially impact current and future biological control agents, including *Euthyrhynchus floridanus* (Pointer) (Pentatomidae), *Podisus mucronatus* Uhler (Pentatomidae), *Podisus saggita* (Fabricius) (Pentatomidae), *Stiretrus anchorago* (Fabricius) (Pentatomidae), and *Zelus longipes* (L.) (Reduviidae), as well as various ant and spider species. Predation on populations of the recently released biological control agent *Boreioglycaspis melaleucae* Moore (melaleuca psyllid, Psyllidae) by various pentatomid and coccinellid species has been observed in the field and may be negatively affected by generalist predators. During host specificity testing and under mass rearing conditions prior to its introduction, *B. melaleucae* was attacked by multiple arachnid species. However, the level of predation observed in the field or under laboratory conditions does not appear to impact colonies in a significant way (P. D. Pratt, pers. obs.; S. A. Wineriter pers. comm.). Studies on other psyllids, *Psylla pyricola* Forester (pear

psyllid) and *Diaphorina citri* Kuwayama (Asian citrus psyllid), have shown that their populations are reduced by generalist predators such as *Chrysopa* sp. (Chrysopidae), *Anthocoris* sp. (Anthicoridae), and *Olla v-nigrum* (Mulsant) (Coccinellidae) (Watson & Wilde 1963; Michaud 2001). Furthermore, Watson & Wilde (1963) and Santas (1987) demonstrated a reduction in psyllid populations by generalist predators. Nevertheless, in each study psyllid populations were suppressed by generalist predators at different levels, suggesting that predicting the acquisition and impact of these predators on introduced biological control agents is tenuous.

During our study, we also collected several parasitic hymenopteran species associated with melaleuca in south Florida (Table 2). Hymenopteran species in Australia parasitized ca. 40% of galls formed by the potential biological control agent *Fergusonia* spp. (gall fly) (Davies et al. 2001). Davies et al. (2001) suggested the impact by *Fergusonia* spp. as biological control agents of melaleuca will likely be reduced due to parasitism from local hymenopteran species in Florida. However, predicting which parasitoids may exploit this or other proposed biological control agents is difficult. Initial steps may include a taxonomic comparison among the co-evolved parasitoids in the agent's native and adventive ranges. For instance, *Cirrospilus* sp. (Eulophidae), *Eupelmus* sp. (Eupelmidae) and *Eurytoma* sp. (Eurytomidae) were collected in Australia associated with *Fergusonia* spp. and during our survey we also collected parasitoids belonging to these genera in south Florida (Goolsby et al. 2001). Unfortunately, species determination was not possible for those reported herein. Due to the diversity of both genera, geographic separation over evolutionary time, and lack of Fergusoninidae in the New World, it is unlikely that the species occurring in Australia and Florida are the same. Other genera found during our survey do not correspond to those genera known to parasitize current and candidate biological control agents in their native range, including *Fergusonina* spp., *B. melaleuca*, *Poliopaschia lithochlora* (Lower) (tube-dwelling moth) and *Lophytoma zonalis* (Rohwer) (melaleuca sawfly) (Jensen 1957; Riek 1962; Burrows & Balciunas 1997; Davies et al. 2001; J. A. Goolsby, USDA/ARS, Aust. Bio. Cont. Lab., pers. comm.). Predictions based solely on this survey may grossly underestimate parasitoid acquisition as additional species may be recruited to the system after introduction of the biological control agent. In the future a more accurate assessment may be obtained by surveying melaleuca for endophagous arthropods and comparing regional species databases or arthropod collections in the native and adventive ranges. Further studies may also include an evaluation of predator and parasitoid arthropod recruitment after the release of new biological control agents.

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TRAPPING YELLOWJACKETS (HYMENOPTERA: VESPIDAE) WITH HEPTYL BUTYRATE EMITTED FROM CONTROLLED-RELEASE DISPENSERS

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ABSTRACT

Numbers of workers of *Vespula pensylvanica* (Saussure) (western yellowjacket) and *V. atropilosa* (Sladen) trapped with heptyl butyrate in Washington increased with greater release of the attractant from vial dispensers, up to an estimated 2.3 milligrams heptyl butyrate per hour. *Vespula germanica* (F.) (German yellowjacket) workers were also captured in significant numbers, and numbers of workers captured increased with increased release of heptyl butyrate, up to an estimated 1.4 milligrams per hour. Numbers of workers of *Vespula squamosa* (Drury) trapped with heptyl butyrate in Oklahoma increased with increased release of heptyl butyrate from dispensers, up to an estimated 3.3 milligrams per hour. Vial dispensers, with holes of 6, 12, 22, and 33 mm diameter in the vial lid, lost 0.42, 1.4, 2.3, and 3.3 milligrams of heptyl butyrate per hour in the laboratory and these rates changed little over a period of 4 weeks, indicating close to a zero order rate of release pattern. Rates of loss of 2 ml heptyl butyrate applied to a cotton ball decreased with exposure time, from an initial rate of 6.0 milligrams per hour to near zero at 16 days post-treatment. Captures of wasps in traps sold commercially might be improved with the use of a controlled-release dispenser.

Key Words: Wasp, yellowjacket, trap, attractant, lure, heptyl butyrate

RESUMEN

El número de trabajadores de *Vespula pensylvanica* (Saussure), la avispa "chaqueta amarilla" occidental, y los de *V. atropilosa* (Sladen) atrapados con el butirato heptílico en el estado de Washington aumentó con una mayor liberación del atrayente en frascos dispensadores, hasta un estimado de 2.3 miligramos de butirato heptílico por hora, los trabajadores de *Vespula germanica* (F.), la avispa "chaqueta amarilla" alemán, también fueron capturados en números significantes, y el número de trabajadores capturados aumentó con la mayor liberación de butirato heptílico, hasta un estimado de 1.4 miligramos por hora. El número de los trabajadores de *Vespula squamosa* (Drury) atrapados con butirato heptílico en Oklahoma aumentó con el aumento de la liberación de butirato heptílico de los dispensadores, hasta un estimado 3.3 miligramos por hora. Los frascos dispensadores, con hoyos de 6, 12, 22 y 33 mm de diámetro en el tapón del frasco, perdieron 0.42, 1.37, 2.3, y 3.3 miligramos de butirato heptílico por hora en el laboratorio y estas proporciones cambiaron poco sobre un período de 4 semanas, indicando una proporción del orden cerca del cero del patrón de liberación. La proporción de pérdida de 2 ml de butirato heptílico aplicado a una pelota de algodón bajó con el tiempo de exposición, desde una proporción inicial de 6.0 miligramos por hora hasta cerca de cero a los 16 días después del tratamiento. La recolección de avispas en trampas para venta comercial puede ser mejorada con el uso de un dispensador de liberación controlada.

Heptyl butyrate is attractive to some species of yellowjackets, and is sold commercially as a lure for traps. Workers of the western yellowjacket, *Vespula pensylvanica* (Saussure), and both queens and workers of *Vespula atropilosa* (Sladen), are captured in large numbers in traps baited with heptyl butyrate (Davis et al. 1969; MacDonald et al. 1973; Landolt 1998). Workers of *Vespula acadica* (Sladen), *Vespula consobrina* (Saussure) (blackjacket), *Vespula germanica* (F.) (German yellowjacket), *Vespula maculifrons* (Buysson) (eastern yellowjacket), *Vespula squamosa* (Drury), *Vespula sulphurea* (Saussure), *Vespula vidua* (Saussure), *Vespula vulgaris* (L.),

and other wasps have also been captured in traps baited with heptyl butyrate (Grothaus et al. 1973; Landolt 1998; MacDonald et al. 1974; Reed & Landolt 2003; Reiersen & Wagner 1975, 1978). These trapping studies indicate a broad-based but variable response of a taxonomic range of yellowjacket species to heptyl butyrate. However, it has been concluded that the chemical is effective primarily in attracting *V. pensylvanica* and *V. atropilosa* and is weak or ineffective as a lure for other species of social wasps (Akre et al. 1981).

The use of heptyl butyrate as a trap lure might be improved by providing a controlled release system for optimizing the amount of the chemical

evaporated from traps. In studies evaluating wasp responses to this chemical in traps, heptyl butyrate has been applied directly to the bottom of the trap (0.25 ml) (Davis et al. 1968, 1969), to cotton swabs (0.4 ml) (Howell et al. 1974), to cotton balls (one to 5 ml) (Davis et al. 1973; MacDonald et al. 1973, 1974; Sharp & James 1979), rubber stoppers (Chang 1988), and in polyethylene caps (Landolt 1998). Currently, measured amounts of heptyl butyrate are applied to cotton balls as a means of baiting traps sold commercially for yellowjackets (Rescue Trap®, Sterling International, Inc., Veradale, WA). Although a dose of one to several ml on cotton has been effective as a lure for the yellowjackets *V. pensylvanica* and *V. atropilosa* (Davis et al. 1973, MacDonald et al. 1973, 1974), there are no published determinations of the relationship between dosage or release rate of heptyl butyrate and captures of wasps in traps. Thus, we do not know how to provide optimum amounts of heptyl butyrate for maximum attraction or capture of wasps in traps.

We report here the trapping of several species of *Vespula* with heptyl butyrate emitted at varied release rates, and the first documentation of worker *V. germanica* and *V. squamosa* response to heptyl butyrate in controlled experiments. This study was designed to test for trapping of *V. pensylvanica* in Washington and *V. squamosa* in Oklahoma as primary pest species. Our long term objective is to improve the efficacy of trapping systems for these pest wasps.

MATERIALS AND METHODS

The Dome trap (yellowjacket trap of Gempler's, Bellevue, WI), was used in all field experiments. This plastic trap is opaque yellow below and clear above, with a bottom entrance through which wasps enter the trap. Traps contained about 200 ml of a drowning solution made of 0.01% unscented dishwashing detergent (Palmolive Concentrated Dishwashing Liquid, Colgate-Palmolive, New York, NY) in water. Polypropylene vials (Nalge Nunc International, Rochester, NY, 15 ml 2118-9050 and 30 ml 2118-0001) were used as a means of dispensing heptyl butyrate (Aldrich Chemical Co., Milwaukee, WI). Ten ml of heptyl butyrate were pipetted onto three balls (ca 2.5 cm diam) of cotton wedged into the bottom half of the vial. Chemical release was through a hole in the lid of the vial. Vials were suspended in the top center of the inside of traps by wire.

A range of release rates of heptyl butyrate was provided by varying the diameter of the hole in the lid of vial dispensers. Comparisons of captures of wasps in traps with varying heptyl butyrate release rates were conducted in both the Yakima, Washington and Tulsa, Oklahoma areas, in order to obtain data for *V. pensylvanica* and *V. squamosa* respectively. The same chemical,

lures, traps, and methods were used for the experiments in both Yakima and Tulsa. A randomized complete block design was used for each test, with each of a series of vial hole sizes (providing a different release rate) represented within each of the five replicate blocks. Holes of different sizes were made using sets of drill bits. The first test compared heptyl butyrate in 15 ml vials with holes of 0, 1.0, 1.5, 3.0, 6.0, and 12 mm diameter. The vial with no hole (0 mm hole diameter) was presumed to not release heptyl butyrate. This test was followed by another experiment comparing heptyl butyrate in 30 ml vials with holes of 1.5, 3.0, 6.0, 12, 22, and 33 mm diameter.

In Yakima, the first test was conducted from 19 to 31 July 2000. Traps were hung on fences, shrubbery, and low branches of trees at a golf course, at a height of 2 m, with 30 m spacing between traps. The second test in Yakima was conducted from 4 to 21 August 2000. Traps were positioned as described above, with some blocks at a golf course and others at a commercial tree nursery.

In Tulsa, Oklahoma, the first test was conducted from 12 September to 6 October 2000, with traps on vegetation on and adjacent to the campus of Oral Roberts University. The second test in Tulsa was conducted from 6 October to 3 November 2000, with traps again on vegetation on and near the campus of Oral Roberts University. At both locations, traps were checked twice per week, and the drowning solution of traps was changed weekly. In Tulsa, heptyl butyrate dispensers were replaced after two weeks. In both locations, trap positions were randomized initially and each time that traps were checked.

Release rates of heptyl butyrate from vials were determined by weighing vials that contained heptyl butyrate at intervals to determine weight loss with time. Weight loss was determined for four replicates of 30 ml vials loaded with 10 ml of heptyl butyrate on cotton balls, and with vial hole diameters of 0, 6, 12, 22, and 33 mm. These vial hole sizes were selected because we sought to determine the range of release rates of heptyl butyrate that are effective in attracting wasps to traps. Weight loss was also determined for cotton balls placed on aluminum foil weighing dishes, with an initial application of two ml of heptyl butyrate to the cotton. Vials and cotton balls were weighed every two or three days over the 3-week period of time following the initial loading of the vials with heptyl butyrate. Vials and cotton balls on weighing dishes were held in a fume hood inside the USDA-ARS Yakima Agricultural Research Laboratory, for the 21 day duration of the experiment. Temperature inside of the fume hood was $22.5 \pm 1^\circ\text{C}$, with the temperature variance likely due to changes in building air handling rates and heating/cooling which could alter both the air flow rate through the fume hood and the ambient temperature.

For each of the four trapping experiments, trap catch data were subjected to a regression analysis (DataMost 1995) to determine if there was a significant positive relationship between numbers of wasps captured and vial hole diameter. Also, data from the first experiment for *V. germanica* in Yakima, Washington, and for *V. squamosa* in Tulsa, Oklahoma were subjected to an ANOVA, with treatment means compared using a paired t test (DataMost 1995), to determine if workers of these two species were captured in significant numbers in traps baited with heptyl butyrate. Weight loss data for heptyl butyrate from cotton balls and from vials were subjected to a regression analysis (DataMost 1995) to determine if there was a significant negative relationship between dispenser age and rate of loss.

RESULTS

In the first field test conducted in Yakima, there was a significant positive regression of numbers of wasps trapped in relation to vial hole diameter, and the greatest numbers of *V. pensylvanica* were captured in traps baited with vials with the largest hole size (12 mm diam) (Table 1). Although numbers of *V. atropilosa* and *V. germanica* captured in this test were small, there was a significant positive relationship between vial hole diameter and numbers of workers trapped for both species (Table 1). Numbers of *V. germanica* workers in traps with vials releasing heptyl butyrate were statistically significant compared to traps with vials that did not release heptyl butyrate (0 mm hole), for the 1.5 mm ($t = 2.33$, $p = 0.02$), 3 mm ($t = 1.79$, $p = 0.05$), 6 mm ($t = 1.92$, $p = 0.04$), and 12 mm ($t = 3.87$, $p = 0.001$) diameter holes in vial lids. In this test, totals of 695 *V. pensylvanica*, 58 *V. atropilosa*, and 106 *V. germanica* workers were captured.

In the second field test conducted in Yakima, there was a significant linear regression of num-

bers of *V. pensylvanica* trapped with all vial hole diameters tested (Table 1). Greatest numbers of *V. pensylvanica* and *V. atropilosa* were captured in traps baited with vials with 22 mm diameter holes, with no increase in catches of these wasps with the largest diameter hole in vials, 33 mm (Table 1). The regression of wasps captured versus hole diameter was more significant for vial hole diameters of 1.5 to 22 mm ($r^2 = 0.98$, $p = 0.002$, $df = 5$), compared to 1.5 to 33 mm. Similarly, there was a significant regression of numbers of *V. atropilosa* trapped with all vial hole diameters tested (Table 1), which was stronger for 1.5 to 22 mm ($r^2 = 0.98$, $p = 0.0015$, $df = 5$), compared to 1.5 to 33 mm. There was not a significant linear relationship between vial hole diameter and numbers of *V. germanica* captured in this test (Table 1). Totals of 5075 *V. pensylvanica*, 172 *V. atropilosa*, 114 *V. germanica*, 18 *Dolichovespula maculata* (L.), 4 *Dolichovespula arenaria* (F.), 2 *Polistes aurifer* Saussure, and 1 *Polistes dominulus* (Christ) were captured in this second test in Yakima.

In the first dose-response test conducted in Tulsa, Oklahoma, there was a significant relationship between vial hole diameter and numbers of wasps trapped and greatest numbers of *V. squamosa* workers were captured in traps baited with vials with the largest hole size (12 mm diam) (Table 2). Also, in this test, numbers of *V. squamosa* workers captured in traps with vials releasing heptyl butyrate were significantly greater than numbers of workers in traps with vials that did not release heptyl butyrate, for vial hole diameters of 1.5 mm ($t = 2.03$, $p = 0.02$, $df = 29$), 3 mm ($t = 2.95$, $p = 0.003$), 6 mm ($t = 4.90$, $p = 1.7 \times 10^{-3}$), and 12 mm ($t = 6.2$, $p = 4.4 \times 10^{-7}$). No other vespine wasps, but six female *Polistes perplexus* (Cresson) and nine female *Polistes fuscatus* (F.) were captured in traps in this test. These numbers were not sufficient for statistical analyses.

TABLE 1. MEAN (\pm SE) NUMBERS OF WASPS CAPTURED PER TRAP PER TRAP-CHECK. TRAPS BAITED WITH HEPTYL BUTYRATE IN POLYPROPYLENE VIALS WITH VARIED HOLE DIAMETERS. YAKIMA, WASHINGTON, 2000.

Test 1, July 19-31	Vial hole diameter (mm)						Regression statistics	
	0	1	1.5	3	6	12	r^2	p
<i>V. atropilosa</i>	0.0 \pm 0.0	0.1 \pm 0.1	0.2 \pm 0.1	0.2 \pm 0.1	0.5 \pm 0.1	1.9 \pm 0.4	0.93	0.002
<i>V. germanica</i>	0.0 \pm 0.0	0.2 \pm 0.2	0.4 \pm 0.2	0.6 \pm 0.3	1.2 \pm 0.6	1.6 \pm 0.4	0.94	0.001
<i>V. pensylvanica</i>	0.0 \pm 0.0	1.3 \pm 0.3	2.4 \pm 0.7	2.5 \pm 0.7	6.8 \pm 2.4	22.0 \pm 7.1	0.95	0.001
Test 2, August 4-21	Vial hole diameter (mm)						Regression statistics	
	1.5	3	6	12	22	33	r^2	p
<i>V. atropilosa</i>	0.1 \pm 0.1	0.3 \pm 0.1	0.6 \pm 0.2	1.0 \pm 0.3	2.6 \pm 0.5	2.3 \pm 0.4	0.84	0.01
<i>V. germanica</i>	0.3 \pm 0.2	0.9 \pm 0.3	0.4 \pm 0.1	1.2 \pm 0.4	1.1 \pm 0.4	1.0 \pm 0.3	0.37	0.20
<i>V. pensylvanica</i>	5.3 \pm 1.4	12.7 \pm 2.3	27.8 \pm 5.5	34.9 \pm 4.0	63.2 \pm 5.1	58.3 \pm 8.2	0.84	0.01

TABLE 2. MEAN (\pm SE) NUMBERS OF WASPS CAPTURED PER TRAP PER TRAP-CHECK. TRAPS BAITED WITH HEPTYL BUTYRATE IN POLYPROPYLENE VIALS WITH VARIED HOLE DIAMETERS. TULSA, OKLAHOMA, 2000.

Test 1, September 12-October 6	Vial hole diameter (mm)						Regression statistics	
	0	1.0	1.5	3	6	12	r ²	p
Wasp species								
<i>V. squamosa</i>	0.2 \pm 0.2	0.3 \pm 0.1	0.9 \pm 0.3	1.3 \pm 0.3	5.5 \pm 1.0	11.2 \pm 1.7	0.99	<0.001
Test 2, October 6-November 3	Vial hole diameter (mm)						Regression statistics	
	1.5	3	6	12	22	33	r ²	p
Wasp species								
<i>V. squamosa</i>	0.4 \pm 0.1	1.1 \pm 0.2	3.1 \pm 0.7	6.3 \pm 1.3	12.3 \pm 2.1	17.8 \pm 3.0	0.99	<0.001

In the second dose-response test conducted in Tulsa, there was a significant positive regression of numbers of wasps trapped with vial hole diameter, up through the largest hole tested, 33 mm, and the greatest numbers of *V. squamosa* captured were in traps baited with vials with 33 mm diameter holes (Table 2). A total of 582 *V. squamosa* workers were captured in the first test in Tulsa, while 1641 *V. squamosa* workers were captured in the second test in Tulsa. No other vespines, but six female *P. fuscatus*, were captured in these traps; not numerous enough for a statistical analysis.

For all vial hole diameters, weight losses from vials were steady over the 28 day duration of the

study (Fig. 1). Y-intercepts of best fit line equations indicated initial release rates (weight losses) of 0, 0.42, 1.37, 2.30, and 3.30 milligrams per hour for vials with holes of 0, 6, 12, 22, and 33 mm in diameter. For vials with holes of 6, 12, 22, and 33 mm in diameter, there was no significant slope (for 6 mm diam holes, r² = 0.05, df = 10, p = 0.49; for 12 mm diam holes, r² = 0.02, df = 10, p = 0.65; for 22 mm diam holes, r² = 0.00, df = 10, p = 0.89; for 33 mm diam holes, r² = 0.25, df = 10, p = 0.12), indicating a near zero order release rate function. Heptyl butyrate on cotton balls was released at a higher rate initially, but decreased over time (Fig. 2). Initial weight losses were near 6 milligrams per hour, decreasing to 5 mg/hr by day 9 and near

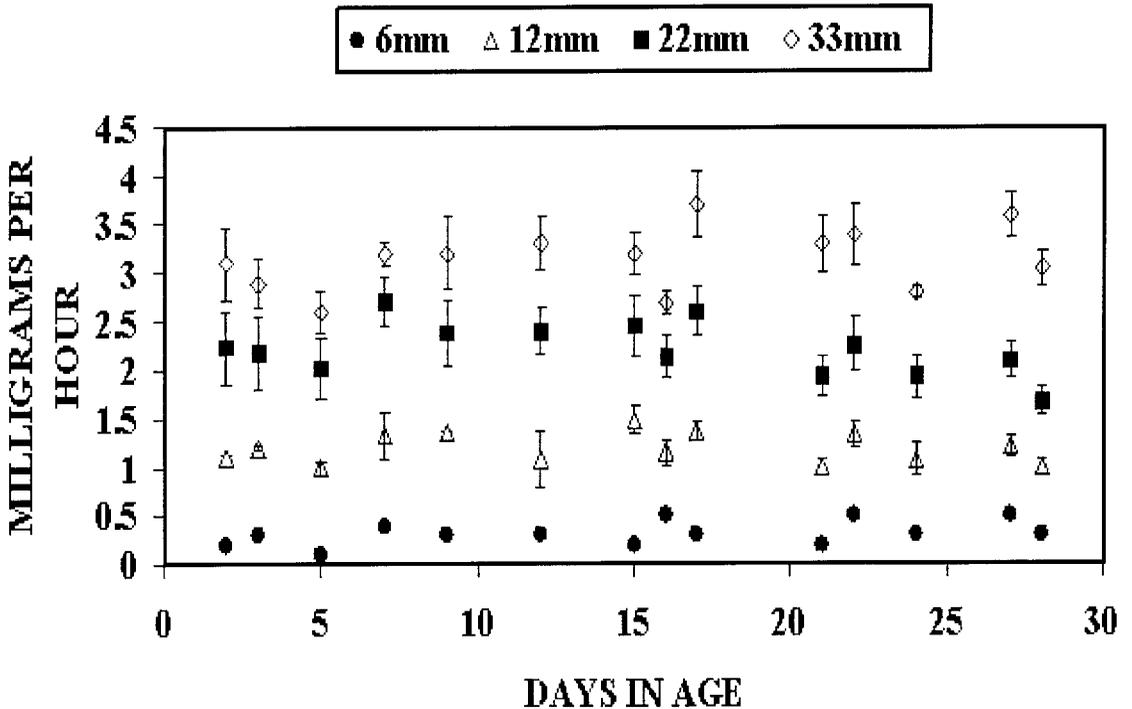


Fig. 1. Mean (\pm SE) milligrams of heptyl butyrate lost per hour from 30 ml polypropylene vials in a laboratory fume hood. Vials had lid holes with diameters of 6, 12, 22, and 33 mm.

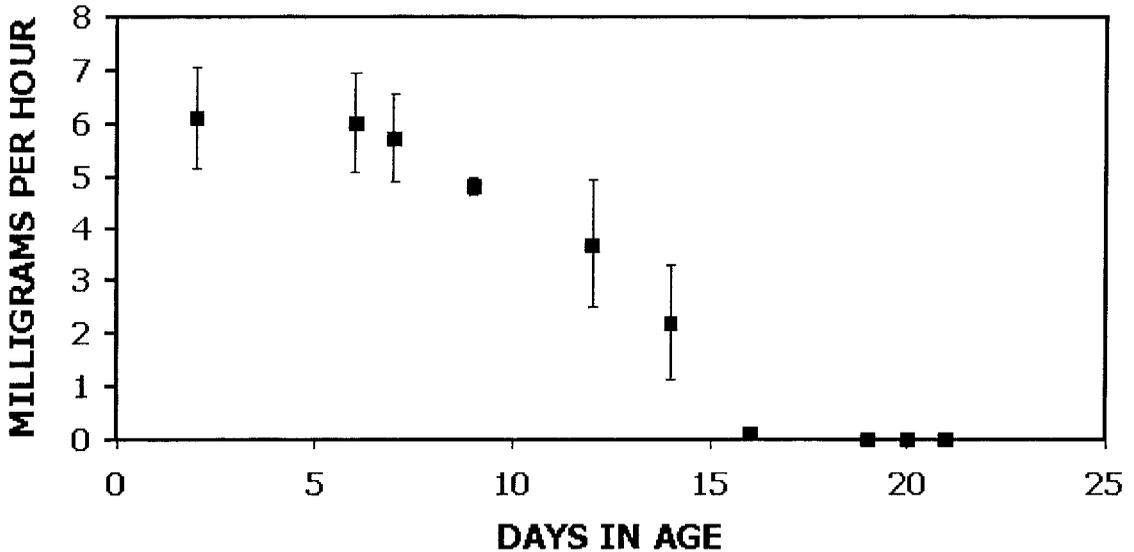


Fig. 2. Mean (\pm SE) milligrams of heptyl butyrate lost per hour from cotton balls in a laboratory fume hood. Cotton balls were soaked with 2 ml heptyl butyrate, and then were placed on aluminum foil weighing dishes.

zero mg/hr by day 16. Rate of loss of heptyl butyrate from exposed cotton balls was related to dispenser age ($r^2 = 0.93$, $df = 9$, $p < 0.01$).

DISCUSSION

These results provide conclusive experimental evidence of worker response to heptyl butyrate for the southern yellowjacket *V. squamosa* and the German yellowjacket *V. germanica*. *Vespula squamosa* is widely distributed in eastern and central North America from the mid Atlantic states to the Gulf of Mexico (Akre et al 1981), and in areas of Central America as far south as Honduras (Hunt et al. 2001). *Vespula germanica* is native to Eurasia, and has become widely distributed and abundant throughout much of temperate North America (MacDonald & Akre 1984; Akre et al. 1989; Vetter et al. 1995). Both species are significant pests. Consistent and significant numbers of *V. squamosa* were captured in this study in traps baited with heptyl butyrate, demonstrating attraction to this chemical. The studies of Grothaus et al. (1973) suggested attractiveness of heptyl butyrate and other chemicals to *V. squamosa*, but did not include unbaited traps or traps that did not release heptyl butyrate as experimental controls, leaving open the question of whether or not *V. squamosa* workers are attracted. Sharp and James (1979) used a mixture of heptyl butyrate and octyl butyrate in their studies of *V. squamosa*, which did not include control traps for comparison. They did not address the question of *V. squamosa* worker attraction to heptyl butyrate, but rather sought to evaluate the attractiveness of trap colors.

A response of *V. germanica* workers to heptyl butyrate was also undocumented prior to this study. Small numbers of *V. germanica* workers were previously captured in traps baited with heptyl butyrate dispensed from a polyethylene cap (Landolt 1998), but unbaited traps were not included in that study as a control. Thus, conclusions could not be drawn regarding the attractiveness of the chemical to *V. germanica*. The experimental demonstration of attractiveness of these wasps to heptyl butyrate with their capture in baited traps does not address the question of the utility of the chemical as a practical means of trapping either species. However, comparisons of heptyl butyrate with lures that release acetic acid and isobutanol indicate a much stronger response by *V. germanica* to the latter attractant (Landolt 1998).

It is of interest, but not known, why numbers of *V. germanica* workers captured in traps in the first test in Yakima increased with vial hole diameter, and yet did not increase with vial hole diameter in the second test in Yakima. Possible variables to consider in future studies are the temperature effects on heptyl butyrate release rates in the field, competitive interactions with other social wasps at or in traps, and changes in responsiveness of *V. germanica* wasps to heptyl butyrate with the advance of the season, or variance in the availability of competing odor sources and food materials.

Greatest numbers of *V. squamosa* workers were captured in traps with heptyl butyrate in vials with the largest hole size tested (33 mm), which gave an estimated rate of loss of about 3.3 milligrams of heptyl butyrate per hour at 22.5°C in the laboratory. It is possible that more *V. squa-*

mosa wasps might be caught at even higher heptyl butyrate release rates.

It has been thoroughly established that very large numbers of *V. pensylvanica* workers can be captured in traps baited with heptyl butyrate (Davis et al. 1969; MacDonald et al. 1973), and results of this work are consistent with those reports. Significant numbers of *V. atropilosa* and *V. germanica* workers were captured in heptyl butyrate-baited traps here, indicating attraction to the chemical. *Vespula atropilosa* has been trapped extensively with heptyl butyrate (Davis et al. 1969; MacDonald et al. 1973). The numbers of both *V. atropilosa* and *V. germanica* captured were dramatically less than the numbers of *V. pensylvanica* captured. The relative differences in numbers of workers captured for different species may reflect both differences in population density at trapping sites and differences in responsiveness to the attractant (MacDonald et al. 1973).

These results provide information that can be used to optimize captures of yellowjackets in traps baited with heptyl butyrate and to provide a means of long-term sustained release of heptyl butyrate at an optimized release rate. An optimum release rate was determined for heptyl butyrate as an attractant for trapping *V. pensylvanica* as well as *V. atropilosa*. Laboratory data indicated release rates (weight losses) of 2.3 and 3.3 milligrams per hour respectively from vials with those hole diameters at laboratory temperatures. The amounts of heptyl butyrate emitted from these vials in the field will change with temperature, wind, and other variable environmental parameters, but these results provide a benchmark for comparison to other types of controlled release technologies and materials. The weight losses of vial dispensers loaded with heptyl butyrate were steady for 30 days for all hole sizes evaluated. Application of heptyl butyrate to a cotton ball (a presently-used commercial application) provided a release rate that was high and likely to be a strong attractant for 6 to 9 days, but changed with time and was reduced to near zero after two weeks, suggesting a relatively short period of attractiveness. The dispensing of heptyl butyrate from a suitable device has the potential of increasing both the attractiveness of the lure to wasps by stabilizing the release rate at a targeted amount and the longevity of the lure at that desired release rate.

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GENETIC VARIATION OF THE SOUTHERN CORN ROOTWORM, (COLEOPTERA: CHRYSOMELIDAE)

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ABSTRACT

Corn rootworms of the genus *Diabrotica* (Coleoptera: Chrysomelidae) are among the most important insect pest of crops in the United States. The southern corn rootworm, *Diabrotica undecimpunctata howardi* Barber is an economically important pest of corn, cucurbits and peanuts. Genetic analysis of southern corn rootworms, collected from South Dakota, Nebraska, and Arkansas was undertaken using DNA sequences of the nuclear ribosomal first internal transcribed spacer region (ITS1), and a portion of the mitochondrial DNA (mtDNA) cytochrome oxidase I and II genes. Among the 22 beetles subjected to DNA sequencing analysis, no polymorphic nucleotide sites were observed for the ITS1 marker and one variable nucleotide site was observed for the mtDNA marker. The lack of genetic distinction observed in southern corn rootworm populations suggests either high levels of dispersal or a recent geographical expansion from a relatively small base.

Key Words: Southern corn rootworm, population genetics, mitochondrial DNA, ribosomal DNA

RESUMEN

Los gusanos de la raíz del maíz del género *Diabrotica* (Coleoptera: Chrysomelidae) están entre las plagas insectiles más importantes en los cultivos en los Estados Unidos. El gusano sureño de la raíz del maíz, *Diabrotica undecimpunctata howardi* Barber es una plaga del maíz, los cucurbitos y de maní económicamente importante. Se llevó a cabo un análisis genético de los gusanos sureños de la raíz del maíz, recolectados en los Estados de Dakota del Sur, Nebraska, y Arkansas usando secuencias del ADN de la primera región espaciadora (spacer region) interna transcrita del ribosoma nuclear (ITS1), y una porción de los genes del citógeno oxidase I y II del ADN mitocondrial (mtADN). Entre los 22 escarabajos sujetos al análisis de secuencia del ADN, no se observaron sitios de nucleótidos polimórficos para el marcador ITS1 y se observó un sitio variable de nucleótido para el marcador de mtADN. La falta de la distinción genética observada en las poblaciones del gusano de la raíz del maíz, sugiere un nivel alto de dispersión o una recién expansión geográfica de una base relativamente pequeña.

Corn rootworms, *Diabrotica* spp., are part of the large group of chysomelid beetles, many of which attack agricultural crops (Levine & Oloumi-Sadeghi 1991). Southern corn rootworm (SCR) *Diabrotica undecimpunctata howardi* Barber, or as adults known as spotted cucumber beetle, is widely distributed in North America, occurring in most areas east of the Rocky Mountains, in southern Canada, and in Mexico. It is most abundant and destructive in the southern United States. This insect is multivoltine and overwinters as adults in the southern parts of its range (Branson & Krysan 1981). Southern corn rootworms infest the roots of many grass crops and weeds, as well as those of peanuts, alfalfa, and occasionally cucurbits. They are most damaging to corn and peanuts. Annually 20 to 25 million acres of corn are treated with soil insecticides to protect the crop from corn rootworm larval feeding damage (Fuller et al. 1997). Soil insecticides applied for the corn rootworm represent one of the major uses of insecticide in the United States. Costs associated with insecticides applied to con-

trol larval damage to corn roots and adult damage to corn silks, along with crop losses can approach \$1 billion annually (Metcalf 1986).

Despite the possible benefits that molecular genetic analysis of SCR may provide towards diagnostics, dispersal, insecticide resistance, and the implementation of area wide control programs, very little research in this area has been conducted. Previous population genetic analysis of SCR is limited to a single study by Krafsur (1999) on allozyme diversity in leaf beetles. An assessment of 56 southern corn rootworms collected from Iowa corn fields using allozymes revealed an average heterozygosity of 11.3% among the 39 loci studied. Although this study did find genetic variation in SCR, the study was directed towards detecting genetic variation in the species and not studying the extent of variation within and among populations.

The goal of our study was to survey population diversity and to determine if molecular marker systems can be used for identifying strains and emerging phenotypes that might affect area wide

control programs. We surveyed two molecular markers, the first internal transcribed spacer region (ITS1), located between the repeating array of nuclear 18S and 5.8S ribosomal genes, and portions of the mitochondrial DNA cytochrome oxidase I and II genes. These markers have been successfully used for monitoring population genetics of western corn rootworm, *D. virgifera virgifera* LeConte (Szalanski et al. 1999) and northern corn rootworm, *D. barberi* Smith and Lawrence (Roehrdanz et al. 2003) and for differentiating *Diabrotica* species (Szalanski & Powers 1996; Szalanski et al. 2000).

MATERIALS AND METHODS

Southern corn rootworm adults were obtained from the field locations as listed in Table 1. Adult rootworms were preserved by immersion in 95% alcohol in the field or transported live to the laboratory and frozen at -80°C. Voucher specimens are maintained at the Arthropod Museum, Department of Entomology, University of Arkansas, Fayetteville, AR.

Alcohol preserved specimens were allowed to dry on filter paper, and DNA was extracted from individual thoraces using the Puregene DNA isolation kit D-5000A (Gentra, Minneapolis, MN). Extracted DNA was resuspended in 50 µl of Tris:EDTA and stored at -20°C. Polymerase chain reaction for the nuclear DNA marker was conducted using the primers rDNA2 (5'-TTGATTACGTC-CCTGCCCTTT-3') described by Vrain et al. (1992), and primer rDNA1.58s (5'-GCCACCTAGTGAGC-CGAGCA-3') by Cherry et al. (1997). These primers amplify a 3' portion of the 18S gene, the entire ITS1 region and a 5' section of the 5.8S gene. The 3' portion of the mtDNA cytochrome oxidase (CO) I gene, tRNA leucine, and a 5' portion of the CO II gene was amplified using the primers C1-J-2797 (5'-CCTCGACGTTATTTCAGATTACC-3') (Simon et al. 1994) and c2-N-3400 (5'-TCAATATCAT-TGATGACCAAT-3') (Taylor et al. 1997). PCR reactions were conducted using 1 µl of the extracted DNA Szalanski et al. (1997). The ITS1 PCR protocol was 40 cycles of 94°C for 45 s, 54°C for 45 s and 72°C for 60 s. The mtDNA PCR protocol consisted of 40 cycles of 94°C for 45 s, 42°C for 45 s,

and 72°C for 60 s. Amplified DNA from individual beetles was purified, and concentrated using Microcon-PCR Filter Units (Millipore, Bedford, MA). Samples were sent to the University of Arkansas DNA Resource Center (Fayetteville, AR) for direct sequencing in both directions using an ABI Prism 377 DNA sequencer. Consensus sequences were obtained from the sequences using GCG Wisconsin Package software (Accelrys, San Diego, CA). GenBank accession numbers for the beetles subjected to DNA sequencing in this study are AY191606 to AY191608. The distance matrix option of PAUP* 4.0b10 (Swofford 2001) was used to calculate genetic distances according to the Kimura 2-parameter model (Kimura 1980) of sequence evolution.

RESULTS AND DISCUSSION

DNA sequencing of the ITS1 PCR-amplified product revealed a 762 bp amplicon for all of the SCR subjected to DNA sequencing (Fig. 1). The average base frequencies were A = 0.37, C = 0.14, G = 0.10, and T = 0.39. Of the 21 SCR individuals sequenced (Table 1), no ITS1 sequences were variable. For the mtDNA COI/COII amplicon, a total of 580 bp were sequenced. The average base frequencies were A = 0.30, C = 0.17, G = 0.20, and T = 0.33. One nucleotide site, 304, was variable among the 21 southern corn rootworm DNA sequences (Fig. 2). One of the SCR sampled from Brookings, SD had a C at this site, while the remaining DNA sequences had a T at this site. To verify this nucleotide polymorphism, the Brookings, SD sample was resequenced in both directions, and all four individual sequences had the polymorphism at site 304. Based on a study by Kobayashi et al. (1999) on PCR error, almost all of the *Epilachna* ladybird beetle mtDNA COI PCR errors, 19 out of 20, were transitions, while the substitution observed in SCR is a transition. In addition, based on the PCR error rate of 7.3×10^{-5} substitutions per site per cycle from Kobayashi et al. (1999), we calculate that the chance of a PCR error at site 304 for two independent PCR amplifications is 8.5×10^{-6} . Based on this, we believe that this nucleotide difference represents an actual polymorphism in the population.

The low level of molecular genetic differentiation within and among SCR populations has been observed in western corn rootworm, *Diabrotica virgifera virgifera* LeConte, and Mexican corn rootworm, *D. v. zeae* Krysan and Smith (Szalanski et al. 1999). No ITS or mtDNA markers were found that were diagnostic for the subspecies despite the fact that there are obvious color differences. What little genetic polymorphism that was detected had no geographical component. Low levels of genetic diversity in the ITS1 and mtDNA regions among widely dispersed populations has been reported for other insect species besides

TABLE 1. SAMPLING LOCATIONS AND DATES FOR COLLECTIONS OF SOUTHERN CORN ROOTWORM.

City	State	n	Year
Dannebrog	NE	5	2001
Lincoln	NE	4	1999
North Platte	NE	1	1996
Brookings	SD	3	1996
Fayetteville	AR	5	2002
Kaiser	AR	4	2002

1 TTGATTACGT *CCCTGCCCTT* *TGTACACACC* *GCCC*GT*CGCT* *ACTACCGTAT*
 51 *TGAATGATTT* *ACTGAGGTTT* *TTCGGACTGA* *GCGCGGTGGC* *GTTTCGGCGT*
 101 *CGTCGATGTT* *TCGAAAGAT* *GACCAAACCT* *GATCATT*T*AG* *AGGAAGTAAA*
 151 *AGTCGTAACA* *AGGTTTCCGT* *AGGTGAACCT* *GCGGAAGGAT* *CATTACAGTG*
 201 *TTGTCAATAA* *ACGACAAGTC* *TGTATTAATT* *ATTT*CG*AACT* *GT*TAAA*ATAA*
 251 *CTGACGTGTG* *TCTTATCTTC* *GTATACTGCA* *AGGAAGAAAA* *ATTAATAGTA*
 301 *ATTAATTATG* *CTTTATTGTG* *GAAAATACGA* *AAAAATAGAG* *ACACATACAC*
 351 *GTGTATTGTT* *ATTATTATTG* *TGATCGTGTA* *GATGCAAAAC* *GTTTTAATGT*
 401 *AATAAATATC* *TCGATAATAT* *ATCGGGTACC* *TAGAGAACGA* *AGTCTTTCGG*
 451 *GATTAGTTCT* *TCGATGGTGA* *TAAAGATTTT* *CGCCCGATTA* *TCAAGAGATG*
 501 *TTACACTGAA* *ACGTAATTTT* *TTGATCGCAT* *TAAGAGAGGA* *AATTCGTGTA*
 551 *CCGTTTTTTTT* *GCACGCCTCG* *TTTGTTTAAAC* *ATATGTGCTG* *TGCTTAAAAA*
 601 *AAAAACGTAA* *TAAACGATTT* *CTTTTCTGAT* *TCGTATAAAAT* *ATACTCGCCA*
 651 *TTTTCTATAA* *ATGACGTTGT* *GTTTCGTACT* *TAAATAAACT* *TTGGGGTTAT*
 701 *AATTTTCGAA* *CGGGACGCGT* *CTAATTAAAC* *GATTACCCTG* *AACGGTGGAT*
 751 *CACTCGGCTC* *GT*

Fig. 1. Nucleotide sequence of the amplified ITS1 region of SCR including portions of the 18S gene (nucleotides 1-177) and 5.8S gene (716-762). Ribosomal gene sequences are in italics, and primer recognition sequences are underlined.

SCR, WCR, and MCR including European corn borer, *Ostrinia nubilalis* (Hübner) (Marcon et al. 1998), stable fly, *Stomoxys calcitrans* L. (Szalanski et al. 1996), and alfalfa weevil, *Hypera postica* (Gyllenhal) (Erney et al. 1996). These species have high mobility or recent expansion from a genetic bottleneck in common. These factors may contribute to the lack of genetic variation among SCR populations.

This is not the case with northern corn rootworm, *Diabrotica barberi* Smith and Lawrence (Roehrdanz et al. 2003). ITS1 DNA sequencing and PCR-RFLP analysis of ITS1 and mtDNA revealed genetic variation within and genetic differentiation among northern corn rootworm populations. With both ITS1 and mtDNA mark-

ers there appeared to be a phylogeographic pattern of genotype frequencies. They observed that populations east of Illinois were homogeneous for one ITS1 genotype, two ITS1 genotypes were observed in Illinois, Wisconsin and North Dakota, while South Dakota, Nebraska, Iowa, and Kansas populations were composed of all three ITS1 genotypes. The mtDNA had 58 haplotypes that displayed a strong east-west geographical partition. The region of overlap occurred in a few counties of east-central Illinois. Possible reasons for this population structure include expansion from different glacial relicts, historic host plant differences, and *Wolbachia* driven reproductive incompatibilities (Roehrdanz et al. 2003). The lack of genetic distinction observed in southern corn rootworm

1 CCTCGACGTT ATTCAGATTA CCCCGATATT TTCATATTAT GAAATATTGT

51 ATCTTCTATT GGATCTCTAA TTTCATTAAT TAGAGTAATC TTCTTAATTT

101 ATATTTTTTTG AGAAGCATT A TCTATAAAAC GTAAAAGATT AAGACCATTA

151 AGATTAACAT CATCAATTGA ATGATTACAA TTTAATCCAC CTGCTGAACA

201 TAGATATTCT GAATTACCAA TACTATCTTC AAATTTCTAA TATGGCAGAT

251 TAGTGCACTG GATTTAAACC CCAAATATAA AGTTTAAACT TTTTTTAGAA

301 ATTTCAACTT GAAAAAATTT CATATTACAA GATAGATCCT **CTCCACTAAT**

351 AGAACAATTA TCTTACTTTC ATGACCATGC ATTAATAAAT CTAGTAATTA

401 TTACAGTATT AGTTGGTCAA TTAATATTTT TTTTATTTTT TAATAAATTT

451 TTACATCGAA ATTTACTTGA AGGACAATTA ATTGAAATTA TTTGAACTAT

501 CCTCCCTACA ATTACATTAA TTTTCATTGC AATTCCTTCA TTACGTTTAA

551 TTTATATTTT AGATGAAGTT AATAACCCAT CTATTACTAT TAAAACTATT

601 GGTCATCAAT GATATTGA

Fig. 2. Nucleotide sequence of the amplified mtDNA COI/COII region of SCR including portions of the COI gene (nucleotides 1-240), tRNA-leu (245-318), and COII gene (322-618). The polymorphic nucleotide site 342 is in bold, and primer recognition sequences are underlined.

populations suggests either high levels of dispersal or a recent geographical expansion from a relatively small base.

The lack of genetic polymorphism in the ribosomal spacer and mitochondrial COI/COII regions diminishes the prospect of using these tools to quickly find molecular markers to track insecticide resistance, or other behavioral modifications in SCR. This is especially relevant given the impending release of genetically modified corn with the *Bacillus thuringiensis* var. *tenebrionis* gene which encodes for an endotoxin specific for Coleoptera, and is targeted towards corn rootworms. Techniques detecting higher levels of polymorphism such as AFLP or microsatellites may reveal markers more suitable for population level analyses of gene flow in SCR. Assays for genes or gene products directly involved may also prove useful, especially for resistance management.

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FIELD RELEASES OF THE DECAPITATING FLY *PSEUDACTEON CURVATUS*
(DIPTERA: PHORIDAE) FOR CONTROL OF IMPORTED FIRE ANTS
(HYMENOPTERA: FORMICIDAE) IN ALABAMA, FLORIDA, AND TENNESSEE

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ABSTRACT

The little decapitating fly, *Pseudacteon curvatus* Borgmeier, was released at 11 sites in Alabama, Florida, and Tennessee as a potential self-sustaining biocontrol agent of imported fire ants. We used a biotype from Buenos Aires Province, Argentina that parasitizes black fire ants (*Solenopsis richteri* Forel). Generally, several thousand flies were released as larvae in parasitized ant workers over a 1-2 week period. *Pseudacteon curvatus* flies were successfully established on hybrid fire ants (*Solenopsis invicta* × *Solenopsis richteri*) at a site near Talladega, Alabama where they have persisted more than two years and expanded out 5-20 km from the original release site. Flies failed to establish in Florida and Tennessee although a few 1st-generation field-reared flies were recovered at four sites in Florida. This fly is only the second parasitoid species to be successfully released against imported fire ants or any other pest ant species. Possible reasons for failures at the other sites include insufficient vegetation cover, competition with another *Pseudacteon* species in Florida, severe winter kill of ants at a site in Tennessee, and the possibility that the biotype of *P. curvatus* released was not a viable parasitoid of red imported fire ants.

Key Words: *Solenopsis richteri*, *Solenopsis invicta*, hybrid fire ants, classical biocontrol, parasitoid, southeastern United States

RESUMEN

La mosca pequeña decapitadora *Pseudacteon curvatus* Borgmeier fue liberada en 11 sitios en Alabama, Florida y Tennessee como un agente auto-sostenible de control biológico de las hormigas de fuego importadas. Usamos un biotipo de la Provincia de Buenos Aires, Argentina que parasita las hormigas negras de fuego (*Solenopsis richteri* Forel). Generalmente, varios miles de moscas fueron liberadas como larvas dentro de las hormigas trabajadoras en un periodo de 1-2 semanas. Las moscas *Pseudacteon curvatus* fueron exitosamente establecidas sobre unas hormigas de fuego híbridas (*Solenopsis invicta* × *Solenopsis richteri*) en un sitio cerca de Talladega, Alabama en donde persistieron por más de dos años y se expandieron 12 km del sitio original donde fueron liberadas. Aunque hormigas de la primera generación criadas en el campo fueron colectadas en cuatro sitios en Florida, las moscas no pudieron establecerse en Florida y Tennessee. Esta mosca es solamente el segundo parasitoide de uso en control biológico que há sido exitosamente liberado para el control de las hormigas importadas de fuego o cualquier otra especie de hormiga. Posibles razones por el fallo en otros sitios incluye insuficiente cubrimiento de vegetación, competición con otras especies de *Pseudacteon* en Florida, una muerte severa invernal de las hormigas en un sitio en Tennessee, y la posibilidad de que el biotipo de *P. curvatus* que fue liberado no es un parasitoide viable de las hormigas rojas de fuego importadas.

Translation provided by Demian Kondo.

When the black imported fire ant, *Solenopsis richteri* Forel, and the red imported fire ant, *Solenopsis invicta* Buren, were accidentally introduced into the United States more than sixty years ago, almost all of their natural enemies were left behind in South America (Jouvenaz

1990). The absence of natural enemies is a likely reason why fire ant densities are 5-10 times higher in the United States than they are in South America (Porter et al. 1992; Porter et al. 1997). Importation of some of the natural enemies left behind in South America (Williams et al.

2002) will hopefully tilt the ecological balance in favor of our native ants (Porter 1998b). If that happens, imported fire ant populations in the United States may decrease to levels similar to those in South America where fire ants are not considered a major problem.

Phorid flies in the genus *Pseudacteon* are one group of natural enemies that have shown some promise in the battle against fire ants (Porter 1998b; Folgarait & Gilbert 1999). One species, *Pseudacteon tricuspis* Borgmeier, is already permanently established in *S. invicta* populations around Gainesville, FL (Porter et al. 2003), five sites in Alabama (Graham et al. 2001), plus additional sites in at least six other states. *Pseudacteon curvatus* Borgmeier is a second species of particular interest. It has been reared in large enough numbers for inoculative releases (Vogt et al. 2003) and it attacks only small fire ants (Morrison et al. 1997). Consequently, it has the potential of greatly complementing the impacts of *P. tricuspis* which only attacks medium and medium-large fire ants (Morrison et al. 1999).

Pseudacteon flies are very host specific (Porter et al. 1995; Porter 1998a; Porter & Alonso 1999; Gilbert & Morrison 1997; Morrison & Gilbert 1999). *Pseudacteon curvatus* can complete development in several species of fire ants in Argentina (Fogarait et al. 2002), but Porter (2000) showed that *P. curvatus* flies from south of Buenos Aires, Argentina were entirely specific to *Solenopsis* fire ants. Additional tests demonstrated that these flies could develop in native fire ants, but at a much lower rate than in imported fire ants (Porter 2000). However, Porter (2000) argued that *P. curvatus* are most likely to benefit native fire ants because these flies are a much greater threat to imported fire ants, which are the number one enemy of native fire ants. A series of host preference tests revealed that *P. curvatus* preferred *S. richteri* and hybrid fire ants when tested against *S. invicta* (Porter & Briano 2000). This preference for black fire ants was not surprising because the biotype of flies tested originally came from an area with black fire ants. However, it was interesting that parasitism rates were not significantly different among red, black and hybrid fire ants in no-choice parasitism tests (Porter & Briano 2000).

The objective of this study was to determine if *P. curvatus* could be successfully released as a biological control agent against imported fire ants in the United States. We were particularly interested in determining whether this fly could be established on populations of red imported fire ants, black imported fire ants and/or their hybrid. This information was especially important for Alabama and Tennessee. About half of Alabama is occupied by black and hybrid fire ants and Tennessee appears to be occupied mostly by either hybrid or black imported fire ants.

MATERIALS AND METHODS

The *P. curvatus* flies used in this study were reared at the USDA-ARS laboratory in Gainesville, FL on red imported fire ants. They were collected from El Toro Ranch east of Las Flores, Buenos Aires Province, Argentina in March of 1997 (Porter 2000). Approximately 1000 parasitized *Solenopsis richteri* ants were originally imported into the Center for Medical, Agricultural and Veterinary Entomology (CMAVE) quarantine facilities in Gainesville, FL.

The flies were released from quarantine in the Fall of 1999 after S.D. Porter obtained permission from the State of Florida and a Finding Of No Significant Impact (FONSI) was issued by the USDA-ARS concerning possible negative impacts on the environment. The FONSI was issued after a select panel of scientists unanimously recommended release. Subsequently, the USF&WS, Region 4 was consulted about the release. State permits were also obtained for field releases in Alabama (K. Flanders) and Tennessee (R. M. Pereira).

Alabama Site

The release site in Alabama was between Atlanta, GA and Birmingham, AL, approximately 3 km east of Talladega, AL (Table 1). Ants at this site were hybrids of *S. invicta* and *S. richteri* as determined by their dark color and cuticular hydrocarbon pattern (Vander Meer et al. 1985). The release site was a 3.6 ha triangular cattle pasture with tall grass and areas of woody shrubs and brambles surrounded on respective sides by a pine forest, a county road, and a small stream. The site gradually sloped down from a well-drained corner to swampy area near the stream.

Mounds at the release site were individually marked with numbered flags. Because cattle tend to pull up flags, a circle was painted on the ground surrounding the mound and a number was painted near the mound. Approximately five grams of workers were collected from each mound and placed into tightly sealed, vented, plastic containers labeled to correspond with the mound numbers. The containers with workers inside were placed into cloth containment bags inside a styrofoam cooler with an ice pack and shipped overnight to the ARS lab in Gainesville, FL on the same day that the ants were collected. Workers were collected from 13 mounds on 8 May 2000, 6 mounds on 10 May, 6 mounds on 17 May, and 13 mounds on 23 May, for a total of 38 mounds over a 15-day period.

Upon receipt in Gainesville, the workers were removed from the containers and allowed to crawl through a number 20 sieve to remove workers too large to be parasitized. One or more groups of 1.0 g of workers were weighed from each colony and each was added to about 1.0 g of brood. Brood was

TABLE 1. RELEASES OF THE DECAPITATING FLY *PSEUDACTEON CURVATUS* AT SITES IN ALABAMA, FLORIDA, AND TENNESSEE.

Site (release dates ¹)	Parasitized ² workers	Colonies used ³ (Gyny ⁴)	Site description
Alabama			
Talladega (13-28 May 2000)	2000	38 HIFA (mono)	Pasture with tall grass, well drained to wet
Florida			
CMAVE (17-31 Jan 2000)	5000	14 RIFA (both)	Around marshy retention pond
Hogtown Cr. (2-14 Feb 2000)	6000	18 RIFA (mono)	Power line right of way
Sanders Farm (16-28 Feb 2000)	7000	17 RIFA (mono)	Suburban horse and cattle pasture
Morrill Farm (1-13 Mar 2000)	7000	17 RIFA (mono)	Cattle pasture with trees and pond
UF Gardens (5-23 May 2001)	1100 ⁵	~25 RIFA (poly)	Roadside and drying sinkhole pond
Natural Area (~10-24 Aug 2001)	>6000	~35 RIFA (poly)	Lawn and around large retention pond
UF Beef Res. Unit (7-14 Sept 2001)	1800	25 RIFA (poly)	Edge of cattle pasture
Tennessee			
Ball Farm, Cleveland (15-29 Apr 2000)	4500	35 HIFA (mono)	Hilly cattle pasture, well drained, rocky
Ames Plantation (31 May-20 Jun 2000)	~4000	27 BIFA (mono)	Cattle pasture in woods with pond
Madisonville (26 Sep-11 Oct 2000)	~4000	23 HIFA (mono)	Edge of large corn/pasture rotation

¹Dates during which parasitized ants were released back into their colonies; these dates are 3-7 days after the ants were collected.

²Approximate number of parasitized workers released, estimated from the number of flies produced from red imported fire ant workers that were retained to maintain colony production.

³The number and kind of fire ant colonies at each site that were used for releases; RIFA = Red Imported Fire Ant (*Solenopsis invicta*), HIFA = Hybrid Imported Fire Ant (Red × Black fire ants), BIFA = Black Imported Fire Ant (*Solenopsis richteri*)

⁴"Gyny" indicates whether colonies at the release site were monogyne (mono) with a single queen or polygyne (poly) with multiple functional queens.

⁵Adult flies were released at this site.

obtained from hybrid fire ant colonies in the laboratory that had been collected several months earlier just south of Chattanooga TN. The presence of sufficient brood is critical, because without it, the workers 'freeze' during fly attacks, making it difficult for the flies to parasitize large numbers of workers.

The groups of workers and brood were placed into large automatic attack boxes similar to the improved version described by Vogt et al. (2003) where they were exposed to attacks by *P. curvatus* flies for 2-3 days. The newly parasitized workers were collected and most of the brood was removed with sorting sheets (Banks et al. 1981) before the workers were repackaged and shipped overnight to Talladega County, AL for release. Within 24 hours of receipt, these workers were released into the same mound from which they were originally removed. This was done by placing the opened plastic shipping container near the side of the mound that had been disturbed sufficiently to cause workers to emerge. Generally, the parasitized workers were recruited back into the mound in 10-20 min. When conditions were hot and sunny, ants were shaded until the ants rejoined their nestmates inside the mound. On one occasion, we were unable to locate a nest for release of the parasitized workers. Release was attempted in a nearby mound under the assumption that the mound had relocated, but the workers were observed to fight, indicating that it was not the orig-

inal colony. Most of the workers released into this mound were assumed to have perished.

The weather conditions during the release and throughout the summer were hot and dry. The summer of 2000 was the second summer of a two-year drought in the area. From May until August, mean daily maximum air temperatures averaged 32.1°C and mean daily maximum 10-cm soil temperatures averaged 26.7°C. Total rainfall during these months was only 153 mm compared to 436 mm under normal weather conditions.

Sampling for *P. curvatus* was conducted by disturbing 5-8 mounds in the release area. Several dozen workers from the disturbed mounds were crushed in the disturbed area of the mound in order to attract the flies more quickly. Mounds were observed for up to one hour for the appearance of phorid flies.

Florida Sites

Pseudacteon curvatus flies were released at four sites around Gainesville, FL in the spring of 2000 and another three sites in the spring and fall of 2001 (Table 1). Approximately 2-7 thousand parasitized ants were released at 6 of the sites over a 1-2 week period. Collection and handling procedures at those six sites were similar to methods described above except that ants did not need to be shipped back and forth. We were able to return them to their colonies within 3-4 days

rather than 6-8 days. The other difference is that we were usually able to collect enough brood along with the workers so that we did not need to use brood from other colonies. Adult flies were released over disturbed mounds at the UF Garden site using protocols similar to those described for *P. tricuspis* (Porter et al. 2003).

We chose to release parasitized fire ant workers at most of the sites rather than adult *P. curvatus* (Porter et al. 2003) because we were able to collect sufficient numbers of minor workers without unduly disturbing the mounds and thus, eliminated several hours of release time in the field each day. More importantly, several trials with adult flies, including the release at the UF Garden site, were not particularly successful. Most of the flies tended to drift away from disturbed mounds rather rapidly so we were only able to maintain fly activity at disturbed mounds for 20-30 min rather than the 90-120 min normal for *P. tricuspis*.

Tennessee Sites

Pseudacteon curvatus flies were released at three sites in Tennessee. The westernmost site, at the Ames Plantation in Fayette and Hardeman counties, was infested with black imported fire ants. The two other sites in east Tennessee, one near Cleveland in Bradley Co. and the other near Madisonville in Monroe Co., were both infested with hybrid fire ants (Table 1). All sites consisted of pastures bordered by woods and a creek or pond. Approximately 4-5 thousand parasitized ants were released at each site over a 2-3 week period. Collection and handling procedures at these sites were similar to methods described above for the Alabama site.

RESULTS

Alabama Site

The search for field-reared *P. curvatus* flies was initiated on June 9, 2000, about 30 days after the first flies were parasitized in the lab. Subsequent visits were made to the site on June 13, 15, 20 and 27 and July 5, 10, 11, 14, and 18, but no flies were observed on any of these trips. All visits to the site were made in the afternoon between 1300 and 1500 hours, except for June 9 when the site was visited at 1000 hours. Observations were conducted for up to one hour. The site was not visited again until August 14 when the first field-reared flies were observed and collected (5 total, 3 collected). These flies were positively identified as *P. curvatus*. Flies were observed at the site again on August 28 and September 14 and 27. Flies were numerous at most mounds disturbed during the September observations.

In 2001, flies were first observed on May 4, approximately one year after they were first re-

leased (5 flies over 2 mounds). Flies were sighted again on May 7. Sites were visited on May 10 and 24, but flies were not found again until July 5 (3 flies over 1 mound).

On August 16, phorid flies were located at 8 of 12 mounds sampled at the release site. Flies were also found at 5 of 8 mounds about 0.5 km north of the release site and 2 of 10 mounds 1.1 km north. No flies were found 0.3 and 0.5 km further north. Flies were not found at sites 0.2, 0.8 and 1.6 km to the south of the release site.

In July, 2002, flies were numerous at the release site. On July 15, flies were located 3.4 km north of the release site. Sites 3.6 and 4.0 km north of the release were searched, and no flies were found. However, flies were found at these two sites on July 17, but not at sites 6.3 and 7.2 km north of the release. By July 25, the flies were found 11.2 miles north at the Talladega Super-speedway. Flies were located 4.8 km south of the release on July 16, but were not found 5.6 or 7.9 km south of the release. Sites 7.9 and 8.0 km south of the release were devoid of flies on August 5 and September 4. On July 17, flies were found 9.0 km southeast of the release on the edge of the Talladega National Forest and may have spread further in this direction. Gates across the forest roads were locked and we were not able to gain access to search further. One site 7.4 km west-southwest of the release did not have any flies present on this date. Flies were located 19.3 km northeast of the on July 18, but were not seen 21.2 or 21.7 km northeast of the release. Temperatures when flies were active ranged from 26.7°C to 36.6°C and activity was observed from 800 hours until 1600 hours.

Florida and Tennessee Sites

We were able to find several 1st-generation field-reared flies at 4 of 7 Florida sites. However, no additional flies were found in subsequent sample dates even though several of these sites were sampled repeatedly for up to 2 years after the initial releases. In Tennessee, no flies were recovered from the field at all. Almost all of the hybrid fire ant colonies at the Madisonville site were killed over the winter due to record low temperatures in November and December of 2000. This record cold may also have been responsible for the failures at the other two sites.

DISCUSSION

The field release of *P. curvatus* flies in Alabama, where the *Solenopsis* hybrid is the prevalent species, was successful. The flies were released during the second summer of a two-year drought and survived the coldest November and December on record in Alabama. Despite these harsh environmental conditions, *P. curvatus* flies

not only survived but spread to 19.3 km northeast and 9.0 km southeast of the release site. This is the first successful establishment of *P. curvatus* in the United States and only the second successful establishment of a self-sustaining parasitoid species against fire ants (Porter et al. 2002).

Releases of *P. curvatus* in Florida and Tennessee were not successful. The reasons for these failures are not certain, but the success rate (1/11) was much lower than that experienced for *P. tricuspidis* in Florida (Porter et al. 2003) and other states (Graham et al. 2001). A likely possibility *P. curvatus* did not establish at the Florida sites is that the fly biotype released was not viable on red imported fire ant populations in Florida because this biotype was adapted to black fire ants in the Buenos Aires region of Argentina where they were originally collected. Laboratory tests showed this fly biotype had a strong preference for black and hybrid fire ants even though they were able to be reared about as well on red fire ants as blacks and hybrids (Porter & Briano 2000). Perhaps in the field, this biotype was unable to locate red imported fire ants in Florida as well as it did hybrids in Alabama. In other words, this biotype may have been functionally too host specific in the field to succeed on red imported fire ants even though it is much less specific with *Solenopsis* species in the laboratory (Porter 2000) than *P. tricuspidis* (Gilbert & Morrison 1997; Porter & Alonso 1999). Nevertheless, recapture of several 1st-generation field-reared flies in Florida demonstrated that at least some flies were capable of host location in the field.

Competition with *P. tricuspidis* flies already at the Florida sites (Porter et al. 2003) could also have been a factor. However, *P. curvatus* parasitizes smaller ants than *P. tricuspidis*. The three sites in Tennessee with hybrid and black fire ants also failed. Heavy winter kill of almost all of the hybrid fire ant colonies likely explains the failure at the Madisonville, TN site. Although no flies had been recovered prior to November 2000, the record cold temperatures may have contributed to failures at the other two sites.

It is also possible that the release techniques used for *P. curvatus* need improvement. Perhaps releasing large numbers of adult flies would be better than releasing parasitized workers, even though *P. curvatus* flies do not stay over disturbed mounds as long as *P. tricuspidis* flies do. Curiously, fewer parasitized workers were released at the successful Talladega site than were released at most of the unsuccessful sites. The successful release site near Talladega, AL had areas of very dense waist-high grass and areas of damp soil. The other release sites may have been too hot and exposed for this *Pseudacteon* species.

Apparently, *P. curvatus* is capable of expanding out of its release site at rates similar to the 10-30 km/yr that has been reported for *P. tricuspidis* in

Florida (Porter et al. 2003). However, impacts of *P. curvatus* on fire ant populations are still unknown. This will be monitored as flies expand out of the successful release site near Talladega, Alabama.

A release of *P. curvatus* was conducted in Mississippi in spring of 2002 and by spring 2003, flies were recovered about 2 km from the release site (Vogt & Street 2003; pers. comm.). *Pseudacteon curvatus* was also released at four sites in Alabama and two sites in Tennessee late summer of 2002 and spring 2003. Flies have been recovered from one site in Alabama and one site in Tennessee (pers. comm.).

Another biotype of *P. curvatus* collected while attacking *S. invicta* in northern Argentina (near Formosa) is currently being reared and evaluated at the USDA-ARS quarantine facility in Gainesville, FL. Hopefully, this new biotype of *P. curvatus* will be more successful on red imported fire ants in Florida than the Buenos Aires biotype.

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INFLUENCE OF ADULT DIET ON THE MATING SUCCESS AND SURVIVAL OF MALE MEDITERRANEAN FRUIT FLIES (DIPTERA: TEPHRITIDAE) FROM TWO MASS-REARING STRAINS ON FIELD-CAGED HOST TREES

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ABSTRACT

Using field-caged host trees, this study investigated the influence of adult diet on the mating success and survival of male Mediterranean fruit flies, *Ceratitis capitata* (Wied.), from two mass-rearing strains. Upon emergence, males from a genetic sexing (temperature sensitive lethal) strain and a bisexual strain were given either a sugar-protein diet (protein-fed) or a sugar-only diet (protein-deprived). Mating trials were conducted using field-caged host trees, and 100 males of a given strain and diet competed with 100 wild males for matings with 100 wild females (all wild flies were given the sugar-protein diet). There was no apparent effect of diet on male mating success for either mass-reared strain. Wild males obtained significantly more matings per replicate than males from either strain on either diet, and the mean number of matings per replicate was similar between protein-fed and protein-deprived males for both strains. In addition, the survival of protein-fed and protein-deprived males was compared over 2- and 4-day intervals on field-caged host trees. Within each mass-reared strain, there was no apparent effect of adult diet on male survival for either test interval. The present findings are compared with similar studies on other mass-reared strains.

Key Words: *Ceratitis capitata*, nutrition, copulation, sterile insect technique

RESUMEN

Utilizando árboles hospederos dentro de jaulas de campo, este estudio investigó la influencia de la dieta del adulto en el éxito de apareamiento y la sobrevivencia de los machos de la mosca mediterránea de la fruta, *Ceratitis capitata* (Wied.), en dos razas criadas en masa. Después de emerger, los machos de una raza genética sexual (letalmente sensible a la temperatura) y una raza heterosexual alimentados con una dieta de proteína-de azúcar (alimentados con proteína) o una dieta de azúcar solamente (privados de proteína). Pruebas de apareamiento fueron conducidos usando árboles hospederos dentro de jaulas de campo, y 100 machos de una cierta raza y dieta competieron con 100 machos silvestres para aparearse con 100 hembras silvestres (todas las moscas silvestres fueron alimentadas con una dieta de proteína-azúcar). No hubo un efecto aparente de la dieta sobre el éxito de los machos para aparearse con cualquiera de las razas criadas en masa. Los machos silvestres aparearon significativamente más veces por réplica que los machos de ambas razas en cualquiera de las dietas, y el número promedio de los apareamientos por réplica fué similar entre los machos alimentados con proteína y los privados de proteína en las dos razas. Además, se comparó la sobrevivencia de los machos alimentados con proteína, con privados de proteína en un intervalo de 2 y 4 días en árboles hospederos dentro de jaulas de campo. Entre cada raza criada en masa, no había un efecto aparente de la dieta del adulto sobre el sobrevivencia de machos en cualquiera de intervalos de prueba. Se comparan estos descubrimientos con estudios similares en razas criadas en masa.

In a series of recent articles, Yuval and his colleagues have demonstrated the importance of adult diet, specifically the inclusion of protein (yeast hydrolysate), on the mating success and longevity of male Mediterranean fruit flies, *Ceratitis capitata* (Wied.). In the initial study, Blay and Yuval (1997) worked with mass-reared flies and found that, in no-choice tests, females mated more readily with protein-fed males than protein-deprived males and that remating frequency was

lower for females that first mated with protein-fed males than protein-deprived males. Subsequently, Kaspi et al. (2000) observed wild flies on field-caged host trees and found that protein-fed males signaled (pheromone-called) and mated more frequently than protein-deprived males. In another laboratory study, Kaspi and Yuval (2000) investigated the influence of adult diet on mating competition among mass-reared males for wild females and found that protein-fed males had a

mating advantage over protein-deprived males. However, protein-fed males were found to have lower longevity than protein-deprived males.

These findings potentially have great importance for sterile male release programs against the Mediterranean fruit fly. While the pre-release diet in current use is a sugar agar gel, the above studies suggest that the addition of protein may significantly enhance the mating competitiveness of mass-reared males and hence the effectiveness of sterile release programs. Before widespread adoption of this dietary change, however, data on other pairwise combinations of mass-reared and wild strains should be gathered to determine the generality and strength of protein-mediated effects on the mating success and longevity of male Mediterranean fruit flies.

The present study investigates the effect of dietary protein on the mating success and longevity of Mediterranean fruit fly males from two mass-reared strains (Vienna-7/Tol-99 and Maui Med-93) in field-caged host trees in Hawaii. This research expands upon an earlier project (Shelly & Kennelly 2002) in which the mating success and longevity of males from one of these strains (Maui Med-93) were measured under laboratory conditions. This earlier study showed that, in trials with wild flies, protein-fed males had a significant mating advantage over protein-deprived males. However, the addition of protein to the diet did not boost the mating success of mass-reared males in competition with wild males or mass-reared males for wild females. In addition, no difference was found in the survival probability of protein-fed versus protein-deprived males from the mass-reared strain. The present study was undertaken 1) to verify these trends under more natural conditions (field-cages) and 2) to gather comparable data for males from a genetic sexing strain (Vienna-7/Tol-99) used widely (e.g., in California and Guatemala) in ongoing sterile insect release programs.

MATERIALS AND METHODS

Study Insects

Wild flies were reared from infested coffee, *Coffea arabica* L., berries collected on the island of Kauai. Fruits were held over vermiculite at 23-25°C, and larval development proceeded *in situ*. Puparia were sifted from the vermiculite 7-9 days after fruit collection, and adults were separated by sex within 2 days of eclosion, well before reaching sexual maturity at 7-10 days of age. Adults were held in plastic buckets covered with nylon screening (volume 5 liters; 100-125 flies per bucket). Wild flies were provided with a mixture (3:1 v/v) of sugar (sucrose) and protein (yeast hydrolysate) and water *ad libitum*, held at 20-24°C and 65-85% RH, and received both natural and artificial light in a 12:12 (L:D) photoperiod.

Sterile males from two mass-reared strains were used in the mating and survival trials. One was a temperature sensitive lethal (or *tsl*) strain (Vienna-7/Tol-99, hereafter referred to as Vienna-7), a type of genetic sexing strain in which females are selectively killed in the egg stage by exposure to high temperature (Franz et al. 1994), obtained from the California Department of Food and Agriculture Fruit Fly Rearing Facility, Waimanalo, Oahu. The other was a bisexual strain (Maui Med-93) produced by the USDA-APHIS Hawaii Fruit Fly Rearing Facility, Waimanalo. Larvae of both strains were reared on standard larval medium (Tanaka et al. 1969), and males from both strains received an absorbed dose of 150 Gy of gamma radiation from a ¹³⁷Cs source 2 days before emergence and then delivered to the laboratory. For the Maui Med-93 strain, males were collected within 12 h of emergence (males of this strain become sexually mature at 2-4 days of age). Mass-reared males were separated into 2 dietary regimes: "protein-fed" males were given the same sugar-protein mixture as wild flies plus water, and "protein-deprived" males were given only sugar plus water. Aside from this dietary difference, mass-reared males were maintained in the same manner as wild flies.

Mating Trials

Mating tests were conducted at the Agricultural Experiment Station of the University of Hawaii, Waimanalo. Groups of 100 irradiated, mass-reared males (from the same strain and diet), 100 wild males (10-15 days old), and 100 wild females (10-17 days old) were released between 0800-0830 h in field-cages (2.5 m in height, 3.0 m in diameter) that contained a single rooted guava, *Psidium guajava* L., tree. For a given trial, we marked only males from one group (i.e., mass-reared or wild) and alternated the identity of the marked group between successive trials. Males were marked 1 day before testing by cooling them for several minutes and placing a dot of enamel paint on the thorax. This procedure had no obvious adverse effects, and males resumed normal activities within minutes of handling. The cages were monitored for 4 h, mating pairs were collected in vials, and the males were identified. For each diet, 11 replicates were run using males from the Vienna-7 strain, and 8 replicates were run using Maui Med-93 males. New flies were used in all replicates.

Survival

Two experiments were conducted to examine the effect of adult diet on survival of males from both mass-reared strains. In both cases, 100 protein-fed and 100 protein-deprived males were released into field-cages when 4 days old (the approximate age of release in control programs).

In the first experiment, no food or water was placed in the field-cages (the guava trees contained no fruits or flowers), and survivors were collected and counted 2 days later. In the second, food and water were placed in the field-cage, and survivors were collected and counted 4 days later. Slices of papaya, *Carica papaya* (L.), and orange, *Citrus sinensis* (L.), fruits were presented in an open-sided, covered container suspended in the canopy, and a water container (500 ml) with an emergent cotton wick was wedged in a branch fork. For a given trial, we marked only males from one group (i.e., protein-fed or protein-deprived) and alternated the identity of the marked group between successive trials. Marking procedures followed those described above. For both mass-rearing strains, the survival experiments were run using the same two caged guava trees, and 12 replicates (6 per tree) were performed for the 2-day test, and 16 replicates (8 per tree) were performed for the 4-day test.

Statistical Analysis

Comparisons of mating success and survivorship were made using the t test as assumptions of normality and homoscedasticity were met in all cases. Tests were performed using SigmaStat Statistical Software (Version 2.0). Means (± 1 SD) are presented.

RESULTS

Diet had no apparent effect on the mating success of males from either the Vienna-7 or Maui Med strains. Wild males obtained significantly more matings per replicate than mass-reared males from either strain held on either diet (Table 1). Also, the mean number of matings per replicate did not differ significantly between protein-

fed and protein-deprived males for either the Vienna-7 ($t = 0.7$; $df = 20$; $P = 0.48$) or Maui Med ($t = 0.2$; $df = 20$; $P = 0.61$) strain. Pooling data across diets, we found no difference in relative mating success between the two mass-reared strains: Vienna-7 and Maui Med-93 males obtained 30.1% and 31.5% of the total matings per replicate, respectively, (proportions were arcsine transformed for analysis; $t = 0.3$; $df = 42$; $P = 0.67$).

Likewise, diet had no detectable effect on survival of males from either the Vienna-7 or Maui Med strains. The mean number of survivors did not differ between the 2 trees used for either diet treatment for either strain (t test; $P > 0.05$ in all cases); consequently, data were pooled across the trees. The number of protein-fed and protein-deprived males surviving did not differ, on average, for either mass-reared strain in either the 2-day or the 4-day tests (Table 2). Independent of diet, there was a significant difference in the number of survivors between the Vienna-7 ($x = 61.5 \pm 16.4$) and Maui Med-93 ($x = 39.6 \pm 11.5$) males in the 2-day test ($t = 5.4$, $df = 46$, $P < 0.001$). A similar trend was observed in the 4-day test (Vienna-7: $x = 42.5 \pm 8.9$; Maui Med-03: $x = 36.9 \pm 8.0$), but in this case the difference was not statistically significant ($t = 1.1$; $df = 62$; $P = 0.26$).

DISCUSSION

The present findings revealed that, in direct competition with wild males for wild females, the addition of protein (yeast hydrolysate) to the adult diet had no detectable effect on the mating success of males from two mass-reared strains. Wild males obtained the majority of matings in all experiments, and, independent of diet, males from both the Vienna-7 and Maui Med-93 strains obtained only about 30% of the total matings. In addition, diet had no apparent effect on the survival of mass-reared males. Within each strain, survival probability was similar between protein-fed and protein-deprived males in both the 2- and 4-day tests. Independent of diet, male survival differed significantly between the strains in the 2-day test, with males from the Vienna-7 having a higher survival probability than males of the Maui Med strain. However, male survival was similar in the 2 strains over a 4-day interval.

As noted above, data on the importance of dietary protein are equivocal. To summarize, the addition of protein to the adult diet has been found to enhance mating success in 1) all cases involving competition between wild males (Kaspi et al. 2000; Shelly et al. 2002; Shelly & Kennelly 2002), 2) only some cases involving competition among mass-reared males (Kaspi & Yuval 2000; Shelly & Kennelly 2002), and 3) no instances involving mass-reared males competing against wild males (Shelly & Kennelly 2002; Shelly et al. 2003; this study). It is not known why dietary pro-

TABLE 1. MATING SUCCESS OF PROTEIN-FED AND PROTEIN-DEPRIVED MASS-REARED MALES IN DIRECT COMPETITION WITH WILD MALES FOR COPULATIONS WITH WILD FEMALES. VALUES REPRESENT MEAN NUMBER OF MATINGS (± 1 SD) PER REPLICATE (N = 11 FOR VIENNA-7 AND 8 FOR MAUI MED-93).

Male type	Matings	t
Wild	18.7 (3.4)	8.6***
Vienna-7: Protein-fed	7.2 (2.8)	
Wild	17.3 (4.0)	5.2***
Vienna-7: Protein-deprived	8.3 (4.2)	
Wild	19.2 (4.1)	5.6***
Maui Med-93: Protein-fed	9.1 (3.8)	
Wild	20.1 (4.6)	5.5***
Maui Med-93: Protein-deprived	9.0 (4.4)	

*** $P < 0.001$.

TABLE 2. SURVIVORSHIP OF PROTEIN-FED VERSUS PROTEIN-DEPRIVED MASS-REARED MALES. VALUES REPRESENT MEAN NUMBER (± 1 SD) OF SURVIVORS (OF 100 INDIVIDUALS RELEASED) PER REPLICATE EITHER 2 (NO FOOD AND WATER ADDED) OR 4 (FOOD AND WATER ADDED) DAYS AFTER RELEASE IN FIELD-CAGES. FOR EACH STRAIN, DATA WERE POOLED OVER THE 2 TREES USED, AND $N = 12$ REPLICATES FOR THE 2-DAY TEST AND $N = 16$ REPLICATES FOR THE 4-DAY TEST.

Strain	Interval	Diet	Survivors	t
Vienna-7	2 days	Protein-fed	61.4 (15.8)	0.03 ^{NS}
		Protein-deprived	61.7 (19.8)	
	4 days	Protein-fed	41.8 (7.5)	0.43 ^{NS}
		Protein-deprived	43.3 (10.5)	
Maui Med-93	2 days	Protein-fed	45.6 (12.3)	1.44 ^{NS}
		Protein-deprived	38.2 (12.2)	
	4 days	Protein-fed	36.5 (9.9)	0.40 ^{NS}
		Protein-deprived	37.2 (7.1)	

^{NS}P > 0.05.

tein has a consistently positive effect on mating success for wild males but not for mass-reared males. C. Lauzon (pers. comm.) suggested that, because they developed on fruit without subsequent exposure to irradiation, wild males possessed a natural gut flora whose growth was greatly stimulated by protein. This proliferation, in turn, may have heightened metabolic processes that increased energy stores available for sexual activities. Available data on this point are inconsistent. Kaspi et al. (2000) found that protein-fed wild males signaled more frequently than protein-deprived wild males, whereas Shelly et al. (2002) found no influence of diet on calling activity. A natural community of gut microbes may have also facilitated synthesis of compounds important in sexual activities (e.g., pheromone precursors). Little data exist on potential dietary influences on long-range, female attraction, but Shelly et al. (2002) found no difference in female visitation between protein-fed versus protein-deprived males in a field-cage test. In contrast to wild males, mass-reared, irradiated males are more likely to lack a natural, microbial community. Consequently, dietary protein may not stimulate key metabolic processes as dramatically as in wild males, and sterile males show no or variable increase in mating frequency as a result.

Data on the effects of dietary protein on male survival are scant and conflicting. In the laboratory, Kaspi and Yuval (2000) found that, after 4 days of feeding, protein-fed males were less likely to survive a 24 h period of starvation (on day 5) than protein-deprived males, whereas Shelly & Kennelly (2002) found that male survival varied independently of diet both when food was available continuously or removed after several days. Here, we found no effect of diet on the survival of mass-reared males in field-caged trees. While a more natural situation, the caged trees, although lacking fruits, flowers, or bird feces, may have

harbored microbial populations as well as insect honeydew and frass on leaf and bark surfaces. These potential food sources would, of course, be available to all males and would therefore act to reduce any nutritional differences that existed between protein-fed and protein-deprived males prior to their release on the tree.

Independent of dietary considerations, the present study once again highlights the need to develop and implement rearing procedures that improve the mating performance of mass-reared males for control of the Mediterranean fruit fly. Similar to other studies (reviewed by Cayol 2000), our results show that, relative to wild males, mass-reared males are poor competitors in the sexual arena. Echoing earlier advice (Calkins 1984), we therefore urge the development of rearing procedures that attempt to increase the quality as well as the quantity of sterile Mediterranean fruit flies produced.

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THE NYMPH OF *SIPHLURISCUS CHINENSIS* AND ADDITIONAL IMAGINAL DESCRIPTION: A LIVING MAYFLY WITH JURASSIC ORIGINS
(SIPHLURISCIDAE NEW FAMILY: EPHEMEROPTERA)

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ABSTRACT

The nymph, female imago and egg of *Siphuriscus chinensis* Ulmer are described and figured in detail for the first time based on associated nymphs and imagos from China. Additional characters of the male imago are described. Based upon imaginal and nymphal characters, Siphuriscidae **fam. n.** is established in the Siphonuroidea for *Siphuriscus* and, provisionally, the Jurassic genus *Stackelbergisca* Tshernova. *Siphuriscus ? davidi* Navás, known from one male subimago, is transferred to *Siphonurus davidi* **comb. n.** The family Siphuriscidae is distinguished from all other families of Siphonuroidea by the presence of coxal gills on the fore and middle legs in all stages and in the nymph by the presence of a basal, moveable, dactyl-like appendage on each claw, and labial and maxillary gills. Characters of the nymphal mouthparts, particularly the mandibles and maxillae, suggest that Siphuriscidae is a sister-group of the family Nesameletidae. However, the majority of character states are considered plesiomorphic in the Ephemeroptera, and may contribute valuable information on the origin, phylogeny and biogeography of Ephemeroptera.

Key Words: *Siphuriscus*, *Stackelbergisca*, Siphuriscidae, phylogeny, China, Jurassic

RESUMEN

La ninfa, adulto hembra y huevo de *Siphuriscus chinensis* Ulmer son descritos e ilustrados en detalle por primera vez basados en ninfas y adultos asociados de China. Características adicionales del adulto macho son descritas. Basados en caracteres del adulto y ninfa, Siphuriscidae **fam. n.** esta establecida en la Siphonuroidea para *Siphuriscus* y, provisionalmente, el genero Jurásico *Stackelbergisca* Tshernova. *Siphuriscus ? davidi* Návas, conocido de un subadulto macho, es transferido a *Siphonurus davidi* **comb. n.** La familia Siphuriscidae es distinguida de todas las demas familias de Siphonuroidea por la presencia de branquias coxales en las patas delanteras y medias en todos los estados y en la ninfa por la presencia de apendices basales, movibles, tipo dactil en cada uña, y branquias labiales y maxilares. Características de las partes bucales de la ninfa, particularmente el de las mandibulas y maxilas, sugieren que Siphuriscidae es un grupo hermana de la familia Nesameletidae. Sin embargo, la mayoría de los caracteres de los estados son considerados plesiomórficos en Ephemeroptera, y pueda contribuir información valuable en el origen, filogenia y biogeografía de Ephemeroptera.

Translation provided by author.

Ephemeroptera (mayflies) are among the oldest orders of insects. The earliest record comes from the Upper Carboniferous (Carpenter 1992; Hubbard 1990; Kukulová-Peck 1983, 1985, 1991; McCafferty 1990; Sinitchenkova 1984), and six extant families have been found from the Jurassic (Hubbard & Savage 1981; Hubbard 1990; McCafferty 1990). Because of fragmentary and incomplete specimens and because usually only one life history stage is known, McCafferty (1990) indicated that among extant families only Siphonuridae *sensu lato* is unquestionably represented from the Jurassic.

In 1967, Tshernova established a new genus and species for the Middle Jurassic species *Stackelbergisca sibirica* based on an imaginal forewing print and relatively well-deposited nymphal parts.

Earlier, Ulmer (1920) had described *Siphuriscus chinensis* from extant male imagos and female subimagos from China. In 1976, Edmunds et al. suggested that *Acanthametropus* might be the immature stage of *Siphuriscus*, but this theory was negated by publication of the imago of *Acanthametropus* by Tshernova et al. (1986). Although Ulmer's specimens were redescribed by Demoulin (1955) and McCafferty & Wang (1994), the nymph remained unknown until the present. Demoulin (1974) grouped *Stackelbergisca* and *Siphuriscus* together based on similarities in the wing and proposed a new unnamed subfamily of Siphonuridae.

A second species, *Siphuriscus ? davidi*, was described by Navás (1932), but only a wing fragment was illustrated and the description was inadequate

for generic placement. From the distribution (Sichuan province, "Se-Tchouen"), body length, and wing venation, this appears to be a species of *Siphonurus*, a genus which the senior author has frequently collected from Sichuan province in western China. Pending its redescription, we treat this species as *Siphonurus davidi* (Navás) **comb. n.**

In 1994, nymphs of an unknown genus of mayflies were collected by the senior author from Zhejiang province, southeastern China, and a male and a female imago of *Siphuriscus chinensis* were collected from nearby localities in 1993 and 1999. Brief notes on these specimens were published by Gui (1994). Upon further study, we were able to associate the nymphs with imagos based on characters not previously discussed in the literature, particularly the existence of coxal gills on the forelegs and middle legs. In addition, the wing venation and abdominal color pattern were the same as that described by Ulmer (1920). In this paper, we provide additional description of the male imago, describe the female imago, nymph and egg for the first time, establish the new family Siphuriscidae, and discuss its relationship with *Stachelbergisca*.

Genus *Siphuriscus* Ulmer, 1920

Siphuriscus Ulmer, 1920:61; Demoulin, 1955: 1; Demoulin, 1974: 4; McCafferty & Wang, 1994: 211.

Nymph [(in alcohol) (Figs. 1-20, 28)]

Head hypognathous, upper portion global (Figs. 1-2). Antennae short, 6-segmented, scape thicker than other segments, apical segment of flagellum hair-like (Figs. 2-3). Clypeus large, lateral margins with indentation (Fig. 2). Mouthparts (Figs. 2-11): labrum with Y-shaped suture on dorsal surface and short setae on margins (Figs. 2, 4). Hypopharynx as in Fig. 5, lingua narrow basally and broadened apically, apical margins of lingua and superlinguae with fine hair. Mandible with large blade-like outer incisor and small spine-like inner incisor; a row of hair between incisor and molar area, and a small tuft of hairs present at apex of mola (Figs. 6-7). Maxillae with distinct galea-lacinia fusion suture; distal portion of galea-lacinia with a row of spines and setae (Figs. 8-9); maxillary palps 3-segmented, basal segment a little longer than 2nd, apical segment small, very short; two tufts of gills on inner and outer basal surface of maxillae (Fig. 8). Labium with long, narrow, unfused glossae and paraglossae, aboral surface with long hair; labial palp 3-segmented, 3rd segment shorter than basal two with small rounded constriction apically (Figs. 10-11); postmentum well-developed, with one pair of gill tufts laterally (Fig. 10). Forelegs and middle legs with coxal gill tufts (Fig. 15); tibia and tarsus of all legs subequal in length, to-

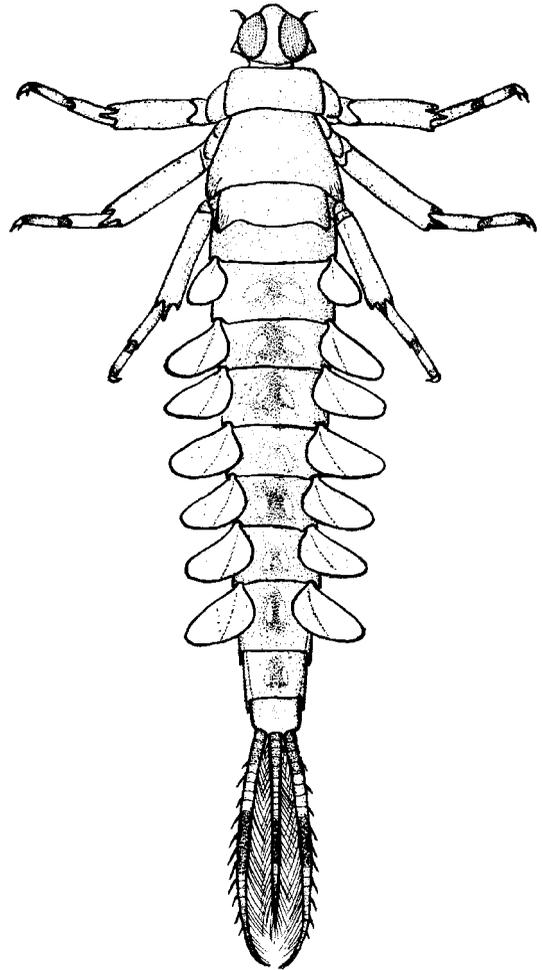
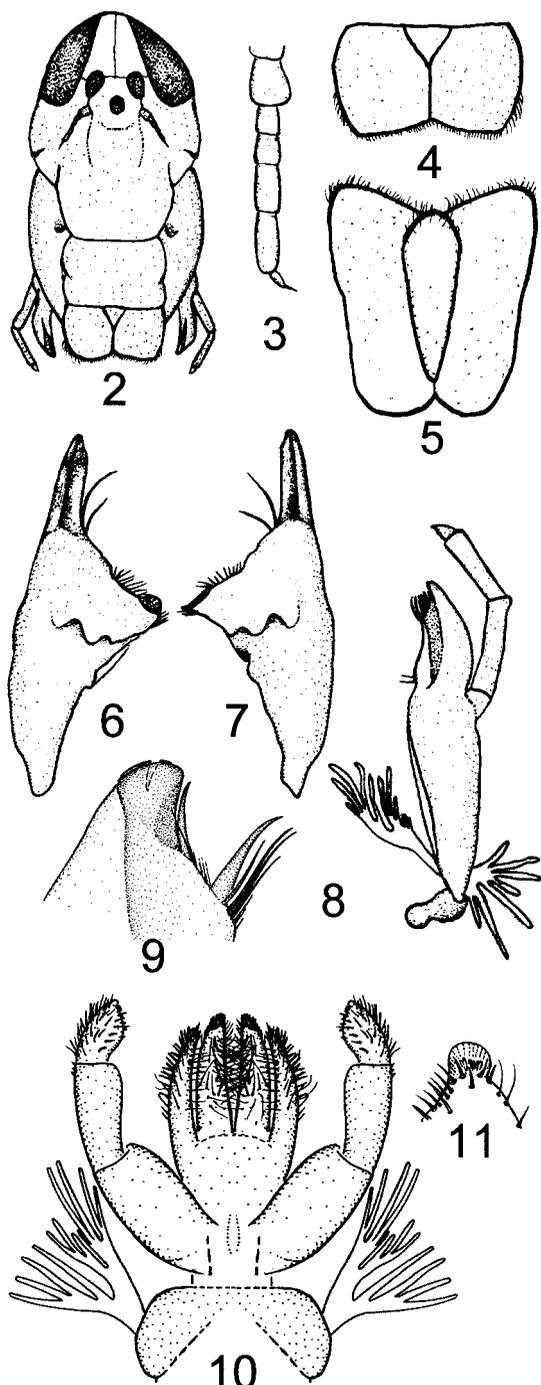


Fig. 1. *Siphuriscus chinensis*, female nymph (habitus).

gether shorter than femur, apex of femur divided into 3 lobes (Figs. 15-17), each with small, stout spines at apex; tibiae of middle and hind legs with patellar-tibial fusion suture; outer margins of all legs with a row of fine hairs (Figs. 15-17). All claws with a broad-based, movable dactyl-like appendage arising from claw base (Figs. 18-19, 28), its inner margin with a row of shallow depressions and its apex long, slender and spine-shaped; inner surface of claw with a shallow groove (Fig. 18). Gills present on abdominal segments 1-7, all gills single, oval, with sclerotized fore costae and submesal sclerotized hind costae (Figs. 1, 12) except costae on first pair of gills small and indistinct (Fig. 14), costae with small blunt setae on surface (Fig. 13); gills 2-7 with small spines apically on anterior margin (Fig. 13); tracheae pigmented. Terga and sterna with very tiny spines on surface, posterior margins of terga with a row of similar spines. Posterolateral projections on ab-



Figs. 2-11. Nymph of *Siphuriscus chinensis*: 2, head (frontal view); 3, antenna; 4, labrum; 5, hypopharynx; 6, left mandible; 7, right mandible; 8, maxilla; 9, distal detail of maxilla; 10, labium (with apex of postmentum); 11, dorsal detail of apex of labial palp segment 3.

dominal segments 1-9 moderately developed into sharp spines, largest on terga 7-9, tergum 10 with concave posterior margin (Fig. 1). Paraproct with

a stout spine on mesal-posterior angle (Fig. 20). Terminal filament shorter than cerci; lateral margins of terminal filament and inner margins of cerci with dense long hairs, each cercus with spines laterally (Fig. 1).

Imago [(in alcohol) (Figs. 21-27)]

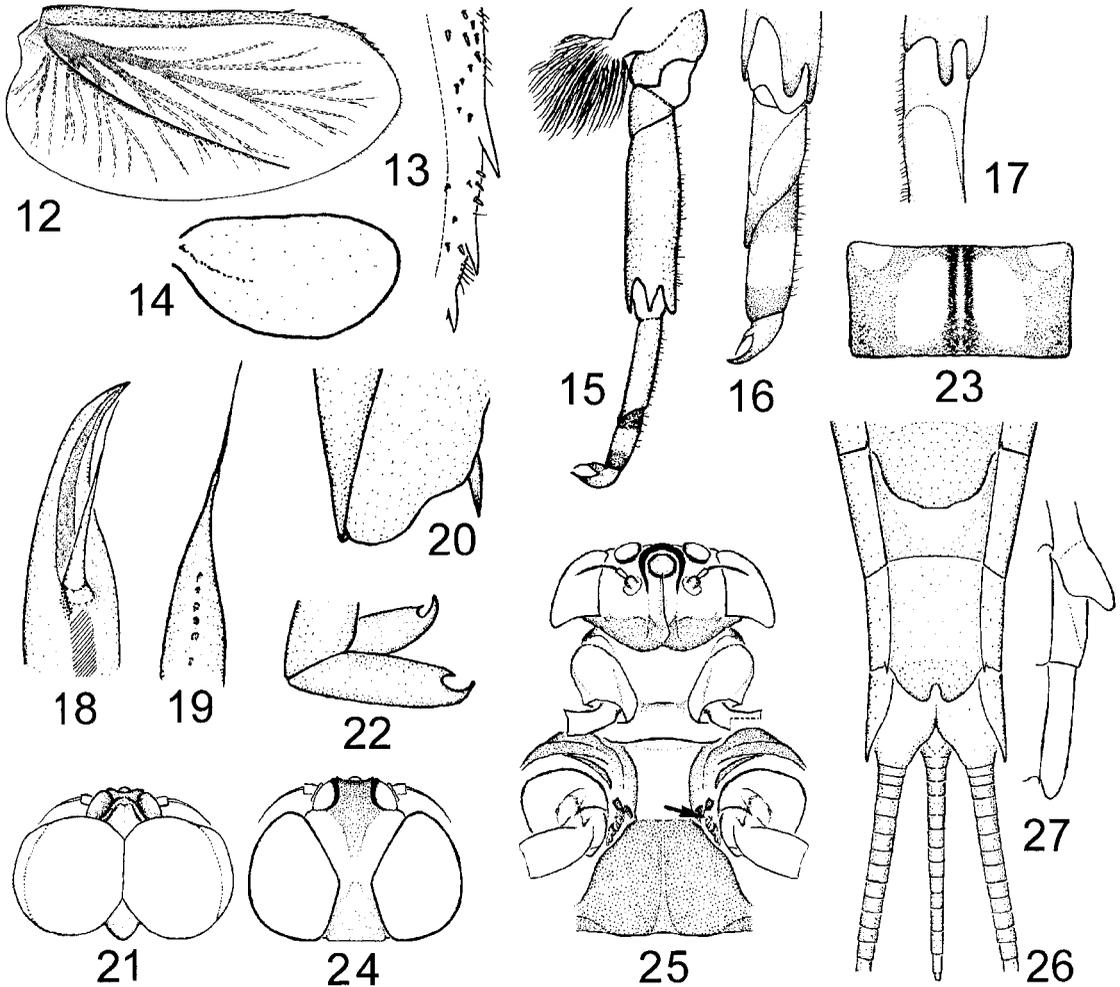
As previously described by Demoulin (1955) and McCafferty & Wang (1994) with following additional characters: compound eyes of ♂ contiguous dorsally, divided into dorsal and ventral portions (Fig. 21); eyes of ♀ separated by width of lateral ocellus (Fig. 24). Head with a horseshoe-shaped carina surrounding median ocellus posteriorly and laterally, a median longitudinal carina running from median ocellus to anterior margin of head (Fig. 25), occiput with posterior projection in ♂ (Fig. 21), broad in ♀ (Fig. 24). Furcasternal protuberances of mesothorax separated posteriorly (Fig. 25). Coxae of fore and middle legs with gill remnants at base (Fig. 25); middle and hind legs with distinct patellar-tibial fusion line; apex of femora of all legs subdivided into 3 lobes. Claws of all legs similar, paired; each hooked, acute with opposing hook (Fig. 22). Ninth sternum of ♀ with concave posterior margin (Fig. 26); sternum 7 of ♀ well developed and extended about half length of sternum 8, median portion of sternum 8 pale, more membranous than surrounding exoskeleton (Figs. 26-27). Terminal filament very short, about 1/10 length of cerci (Fig. 26).

Egg [(description from T. Soldán) (Figs. 29-31)]

Oval, about 1.3 times longer than wide, measurements: 243 μm (238-252 μm) \times 188 μm (185-200 μm), 16 eggs measured. Approximately 15-24 loose attachment structures irregularly scattered around poles, but absent at the poles (Figs. 29-31). Attachment structures measuring 10-35 μm and consisting of two subunits: proximal part elongated, funnel-like, about 3-5 times wider apically than at base; distal part regularly oval or globular, measuring about 7-12 μm in diameter (Fig. 30). Attachment structures similar in length and shape at both poles, but globular distal subunits about twice as wide in diameter on one of the poles. A single micropyle submedial to attachment structures in all eggs examined (Fig. 30). Micropyle roughly oval, bluntly pointed at one side, measuring 10-12 μm \times 15-16 μm ; micropylar rim not developed; sperm guide inconspicuous, connected to bluntly pointed portion of micropyle, measuring about 7.5 μm . Exochorionic surface uniform, consisting of irregular rounded or oval granulation 2.5-4.5 μm in diameter.

Species Included

Siphuriscus chinensis Ulmer.



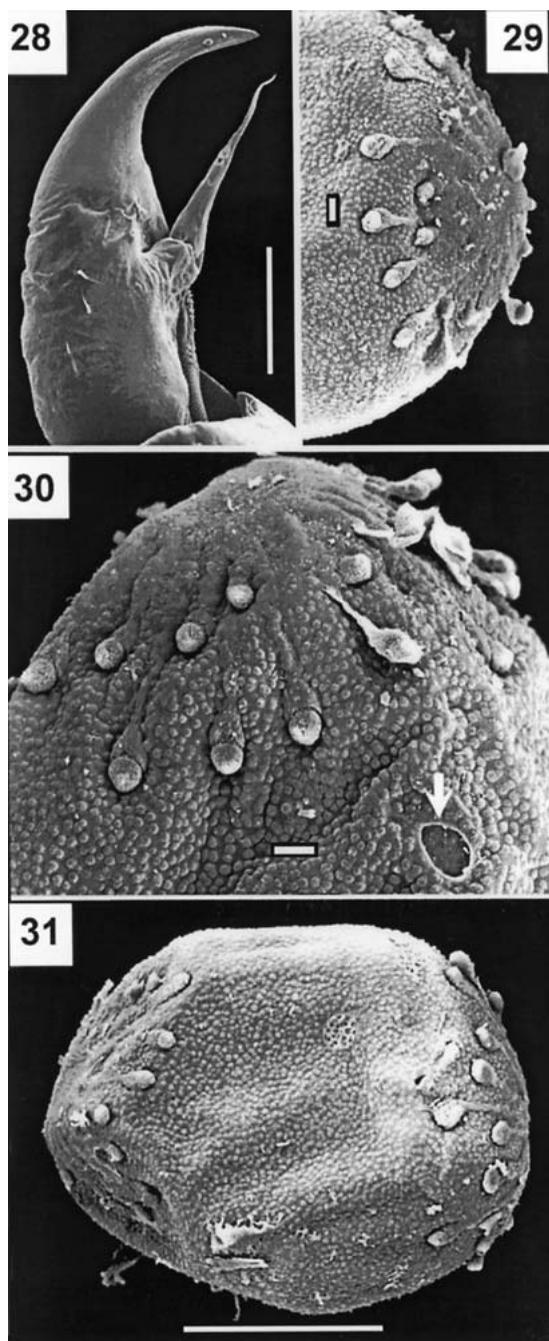
Figs. 12-27. *Siphuriscus chinensis*. Figs. 12-20, nymph: 12-13, gill 4 with apical detail of gill costa (13); 14, gill 1 (tracheation not drawn); 15, foreleg; 16, distal segments of middle leg (ventral); 17, connection between tibia and tarsus of middle leg (dorsal view); 18, apical portion of foreclaw (schematic showing position of groove); 19, detail of dactyl-like appendage of claw; 20, apex of paraproct and margin of tergum 10. Figs. 21-23, male imago: 21, head; 22, foreclaw; 23, tergum 2. Figs. 24-27, female imago: 24, head; 25, pro- and mesosternum (arrow points to gill remnant); 26, sterna 7-9 and caudal filaments; 27, lateral view of sterna 7-9.

DISCUSSION

Siphuriscus is distinguished from all extant genera of Ephemeroptera in the imagos by the combination of straight penes without accessory structures, the deeply divided styliiger plate, the 'siphonuroid' forewing with an exceptionally long and narrow cubital field (as in the Middle Jurassic *Stackelbergisca*), long hind wings (more than half length of forewings), gill remnants on fore and middle coxae, and similar claws. In the nymph, the labial gills, the constricted 3rd segment of the labial palp, and the claws are unique among Ephemeroptera. We believe these characters are sufficiently distinct to follow the recommendation of Demoulin (1974) and establish Siphuriscidae

fam. n. [type genus *Siphuriscus* Ulmer, 1920] for *Siphuriscus* and, provisionally, the Jurassic *Stackelbergisca*, although details of *Stackelbergisca* are not well known (discussed below).

McCafferty & Wang (1994) analyzed relationships between imagos of *Siphuriscus*, *Acanthametropus*, *Analetris*, and Siphonuridae (in the broad sense), showing that *Siphuriscus* was not closely related to the specialized genera included in the psammophilous Acanthametropodidae; they considered the deeply forked MA in the hind wing to be an apomorphy of *Siphuriscus*. Kluge et al. (1995) then summarized relationships of all the family groups where both adults and nymphs were known. Although lacking details of the sub-imago cuticle, we refer to Kluge et al. (1995) for



Figs. 28-31, *Siphuriscus chinensis*. Fig. 28, nymphal claw. Figs. 29-31, egg: 29-30, polar regions of egg with detail of attachment structures and micropyle (Fig. 30, arrow); 31, whole egg. (SEM scale bar = 100 μm in Figs. 28, 31; 10 μm in Figs. 29, 30).

most comparative data. Siphuriscidae share a few common characters with genera of the Northern Hemisphere Siphonuridae and Ameletidae. However, the closest relationship would appear to

be with the Southern Hemisphere Nesameletidae where at least seven of the character states discussed by Kluge et al. (1995) are of similar structure (elongated mandibles with long incisor, modified setae on apex of maxilla, short third segment of maxillary palp, long and narrow unfused glossae and paraglossae, unpaired projection on occiput of male imago, well developed subgenital plate on female sternum 7, and similar adult claws). *Siphuriscus* is easily distinguished from all genera of Nesameletidae in imagos by the greater length of the hind wing ($> \frac{1}{2}$ length of forewing), the deeply divided male styliger plate, penes joined only at base, and the basally forked MA vein in the hind wing; and in the nymph by the presence of well-developed maxillary and labial gills, gills on the pro- and mesothoracic coxae and the unique claw.

Any attempt at cladistic analysis of families within Siphonuroidea is complicated by the fact that the group as presently defined is distinguished by a complex of plesiomorphies (Kluge et al. 1995). In *Siphuriscus*, imaginal structures are considered either plesiomorphic, subject to frequent reversal, or derived by reduction or fusion. Based on the work of paleontologists and morphologists (Smith 1969; Kukulová-Peck 1991, 1992; Gaino & Rebora 1995), we know that the penes of insects have evolved through the loss or fusion of what were ancestrally complex structures and the simpler structure of the penes of *Siphuriscus* would be considered derived, but such reductions are found throughout the order. Similarly, the blade-like outer incisor of the mandible represents a highly specialized algal scraping device found in mayfly nymphs of other families and immature stages of other insect orders; it is considered the most common type of feeding specialization found in immature aquatic insects (Arens 1990). The inner incisor (termed "kinetodontium" by Kukulová-Peck 1991 and Kluge 2000) appears as a spine inserted at the base of the outer incisor ("canine") and its evolutionary status is unclear. Gills at the base of mouthparts and coxae, sometimes called accessory gills to distinguish them from the plate-like abdominal gills (tergaliae of Kluge et al. 1995), are broadly distributed in Ephemeroptera nymphs and persist into the adult stage of several genera of Ephemeroptera, Plecoptera, Odonata, and Trichoptera (Štys & Soldán 1980). The historical evolution of the paraproct has never been studied in Ephemeroptera, but the paraproct of *Siphuriscus* is presumably plesiomorphic based on available outgroups because an acute submedial spine or projection is also found in Siphonuridae, Metretopodidae, Oniscisgastridae and Rallidentidae.

Of the characters discussed in Kluge et al. (1995) and McCafferty & Wang (1994), none will clearly align *Siphuriscus* with other extant families, although initial analysis (Table 1) shows a

TABLE 1. CHARACTER STATES OF SIPHLURISCIDAE, SIPHLONURIDAE, AND NESAMELETIDAE.

Character ¹	Ancestral	Derived	Derived in ²	Source ³
Claw (N)	double (apparently)	single	Siphlo; Nes	A1, A2
Hind: forewing length ratio (A)	>1/2	<1/2	Siphlo; Nes	A1, A2, A3
Hind wing MA fork located (A)	medially or distally	basally	Siphur	B
Prosthecae of mandible (N)	present (w/ brush)	reduced or absent	Siphur; Nes	C, F
Setae on apex of maxilla (N)	free	some fusions	Siphur; Nes	C, D
Penes of male (A)	w/ auxiliary structures	simplified	Siphur; Nes	A1, E
Styliger plate of male (A)	divided	fused	Siphlo; Nes	A1, G
7th sternum of female (A)	simple or extended	with pouch	Siphlo	C
Gill costae (N)	with 2 costae	hind costa weak	Siphlo	C

¹Stage indicated as N (nymph) or A (adult).

²Families abbreviated as Siphlo (Siphonuridae), Nes (Nesameletidae), Siphur (Siphuriscidae).

³Sources: A1, Kukulová-Peck 1991, 1992; A2, Tshernova 1967; A3, Demoulin 1974; B, McCafferty & Wang 1994; C, Kluge et al. 1995; D, Kluge 1998 (see paper for explanation of character); E, Gaino & Rebera 1995; F, numerous authors; general consensus; G, this paper.

potential relationship with Nesameletidae. Table 1 gives a brief summary of characters for which there is general agreement in the literature, and ignores for now the many characters (such as accessory gills) open to more than one interpretation. More detailed analysis is needed to determine if characters such as the structure of apical maxillary setae (Kluge 1998) and the structure of the incisor are synapomorphic. Of all nymphal characters of Siphuriscidae, the most interesting and least understood is the claw. It does not resemble the apically bifurcate foreclaw of Metretopodidae, and only one similar claw is known in Ephemeroptera—that of certain Jurassic nymphs found in association with the imago of *Stackelbergisca sibirica*.

Stackelbergisca includes the type species *S. sibirica* described from the holotype wing (indistinguishable from *Siphuriscus*) and *S. shaburensis* Sinitshenkova. At least two different nymphal types have been associated with the *S. sibirica* imago and *S. shaburensis* is described from nymphs only (Sinitshenkova 1991). Some nymphs (*S. sibirica* in part) have a dactyl-like appendage basally, and others do not (*S. sibirica* in part and *S. shaburensis*), and some have small paired projections on posterior abdominal terga and others do not. The presumed mandibles of *Stackelbergisca* are also not clearly associated with a specimen (Tshernova 1967). From this, we can only conclude that some nymphs with a second basal dactyl-like appendage are present in the same formation as *Stackelbergisca* imagos. Although full double claws are clearly the ancestral state in Ephemeroptera (Kukulová-Peck 1968), the illustrated fossil claw of *Stackelbergisca* does not display enough detail to make any definitive determination of its relationships. Thus, the placement of *Stackelbergisca* in Siphuriscidae is provisional, a placement first suggested by Demoulin (1974) based only on the imaginal wing.

The discovery of the similar nymphal claw which has possibly been retained for more than 100 million years reinforces this placement.

If the relationship between *Siphuriscus* and *Stackelbergisca* is correct, we can say that the *Siphuriscus* lineage arose in the Jurassic, and is a representative of the oldest known extant family with regard to the fossil record. *Stackelbergisca* is among the oldest fossils of Siphonuridae *sensu lato* (Carpenter 1992; Hubbard 1990; McCafferty 1990). However, there are many plesiomorphies in Siphonuridae *sensu stricto* (Table 1) and one other genus from the Jurassic (*Oligisca* Demoulin, 1970, known only from a forewing) is assigned to Siphonuridae *sensu stricto*. The Chinese Siphonuridae have yet to be studied, and discovery of the nymph of species such as *Siphonurus davidi* may require a reevaluation of this hypothesis.

Nelson & Platnick (1984) used some mayfly distribution information provided by Edmunds (1981) as evidence to support the geographic congruence between South America, Australia and New Zealand. Kluge et al. (1995) suggested a Northern Hemisphere (Laurasian) origin for the Southern Hemisphere (Gondwanian) Siphonuroidea. Based upon present findings, their arguments should be qualified because the ancestor of extant Nesameletidae may have had a much broader distribution than previously known. The present distribution [Nesameletidae: *Nesameletus* (New Zealand), *Ameletoides* (Australia), *Metamonius* (Chile, Argentina); Siphuriscidae: *Siphuriscus* (Southeastern China), *Stackelbergisca* (Eastern Siberia)] implies that the ancestor of Nesameletidae and Siphuriscidae may have originated in an ancient, continental mass in the paleo-Pacific region and gives support to the hypothesized Pacifica continent proposed by Nur & Ben-Avraham (1977).

The claw could also represent a more recent, independently evolved structure. The limited series of specimens available to us are sufficient for de-

scription and diagnosis, but many questions remain. The functional morphology of the claw cannot be studied without fresh or living material, and almost nothing is known of the biology of the species. Further study of *Siphuriscus* is essential to understand its biology and evolutionary history.

Siphuriscus chinensis Ulmer, 1920

Siphuriscus chinensis Ulmer, 1920: 62 (male imago, subimago); Demoulin, 1955:1 (subimago); McCafferty & Wang, 1994: 211 (male imago and subimago).

Male imago [(in alcohol) (Figs. 21-23)]

Body length 23 mm; forewing 23 mm; hind wing 13 mm; foreleg 17 mm; middle leg 10 mm; cerci 40 mm; terminal filament 3.5 mm. Compound eyes with gray to dark gray dorsal portion and brown ventral portions. Head and thorax dark brown. Body dark brown with yellowish marks; abdominal terga 1-8 as in Fig. 23, each tergum with pair of yellowish marks and median dark brown stripes. Wings transparent, veins dark brown; Sc and Rs of forewing with distinct vein bullae. Forelegs light brown to brown, femora paler than tibiae and tarsi; middle and hind legs slightly paler than forelegs, femora almost similar to tibiae and tarsi in color. Tergum 10 with slight concave posterior margin. Terminal filament paler than cerci, all filaments with tiny brown setae on surface.

Female imago [(in alcohol) (Figs. 24-27)]

Body length 24-25 mm; forewing 24-25 mm; hind wing 13.5 mm; foreleg 11.5 mm, middle leg 10.7 mm, hind leg 9.5 mm; cerci 38 mm, terminal filament 3 mm. Similar to male, but body paler, venter and thorax yellowish brown. Terga with similar color pattern as male, but paler. Sterna yellowish, each sternum with a pair of indistinct gray marks on median portion, each mark with pale dots. Last ventral abdominal segments shown in Fig. 26.

Nymph [(in alcohol) (Figs. 1-20, 28)]

Body length 22-24 mm, cerci 7.5 mm, terminal filament 6 mm. General color pale yellowish with indistinct brown marks (in life, yellowish green with reddish stripes). Ocelli gray (Fig. 2). Incisors of mandibles strong, reddish. Apex of tibiae yellowish brown; tarsi with 2 brown bands on basal and distal portions (Figs. 15-16). Each tergum with a pair of pale submedian marks, median area dark, especially on terga 2-3, 6 and 8-9 (Fig. 1). Basal and middle portions of caudal filaments with yellowish brown bands (Fig. 1); apically from basal band, every 4th annulation of cerci with spines on outer lateral margin, 10 of them distinct.

Material

P.R. CHINA: 15 nymphs, Zhejiang Province, Guan-Pu-Yang, Nang-Ju, Long-Quan county (28.04°N, 119.08°E), 600 m, 15-VIII-1994, leg. ZHOU Chang-fa & ZHU Chao-Dong; 1♀, Zhejiang Province, Bai-Shan-Zhu, Qingyuan county (27.37°N, 119.04°E), 20-IX-1993, leg. WU Hong; 1♂, Zhejiang Province, Tian-Mu-Shan mountain (30.26°N, 119.34°E), 2-VI-1999, leg. ZHAO Ming-Shui (13 nymphs, 1♂, 1♀ deposited in Department of Biology, Nanjing Normal University, P.R. China; 2 nymphs in Florida A&M University, USA). Egg from 1♀ collected at light trap, Zhejiang Province, Long-Wan-Shan mountains (30.28°N, 119.22°E), 3-VI-1999, leg. Ignac SIVEC, deposited in the Institute of Entomology, Academy of Sciences of the Czech Republic, České Budějovice.

Biology

The nymphs were collected in quiet water of a small mountain stream with a sand and stone substrate. Width of the streambed was between 2 m and 4 m, but at the time of collection the stream was only about 1 m wide and less than 40 mm deep. The stream is in an undisturbed mountainous area with large trees on the bank, and sunlight reaches the water surface only at noon and early afternoon. Living nymphs can jump quickly like small fish when removed from water. They are strong swimmers and can hold tightly to branches or stones with their legs and claws. Gills of observed nymphs did not move. Mayflies collected from the same stream included *Vietnamella*, *Serratella*, *Isonychia*, and some baetid and heptageniid species.

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POTENTIAL FOR BIOLOGICAL CONTROL OF THE LOBATE LAC SCALE,
PARATACHARDINA LOBATA LOBATA (HEMIPTERA: KERRIIDAE)

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ABSTRACT

The lobate lac scale insect, *Paratachardina lobata lobata* (Chamberlin) (Kerriidae: Coccoidea: Hemiptera), a recent invader of southern Florida from India and Sri Lanka, now infests more than 160 economic and native plants in at least 49 plant families. It is killing wax myrtle (*Myrica cerifera* L.) and coco plum (*Chrysobalanus icaco* L.), valued native and horticultural plants in many locations. Intensive insecticide use in infested natural and residential areas is an unsuitable control approach because of the large numbers of plants infested, the high cost, and probable damage to non-target organisms. Biological control is a much needed solution for lobate lac scale. No parasitism has been detected in Florida. The lobate lac scale is native to India and Sri Lanka, occurring in localities south of 16 degrees N. latitude. The known host range includes some of the same species and families of host plants as it does in Florida, plus other plant groups on which it has yet to be detected in Florida. The natural enemies of the lobate lac scale have not been previously sought nor studied, but those of the related true lac scale of commerce are relatively well known, and some of these appear to have potential for biological control of the lobate lac scale. The most important natural enemies are predaceous Lepidoptera and *Chrysopa* species, and parasitic encyrtid and euplophid chalcidoid wasps. The chalcidoid wasps, with narrower host ranges, appear to be more suitable as potential biological control agents. Among these, *Tachardiaphagus tachardiae* Howard (Encyrtidae), seems particularly promising. It attacks the lobate lac scale, is known only from lac scale hosts, is not hyperparasitic, is one of the most important parasitoids of lac scale, has 9-12 generations per year, and occurs in the same climatic conditions as occur in southern Florida. It is recommended that this wasp and two other important parasitoids of the true lac scale, *T. somervilli* Madhiahassen (Encyrtidae) and *Coccophagus tschirchii* Madhiahassen (Eulophidae), be acquired and evaluated as potential biological control agents of the lobate lac scale. Explorations for unknown natural enemies of lobate lac scale in India and Sri Lanka should also be undertaken in locations with climatic similarity to that of southern Florida. Host specificity testing of species belonging to Florida's 12 native scale families (Coccoidea) and allied Hemiptera is advisable to define the potential host ranges and thus the safety of candidate biological control agents. The prospects of effective and safe biological control appear to be good. No native lac scales (Kerriidae) occur in Florida, and parasitoids are known that appear to be both narrow specialists and damaging to their host lac scales.

Key Words: New pest, native plants, fruit trees, ornamental plants, lac scales parasitoids, *Kerria lacca*, Everglades National Park, Big Cypress NWR, Florida, India

RESUMEN

La escama lobulada de la laca, *Paratachardina lobata lobata* (Chamberlin) (Kerriidae: Coccoidea: Hemiptera), un invasor reciente en el sur de la Florida y proveniente de la India y Sri Lanka, ahora infesta más de 160 plantas nativas y económicas en por lo menos 49 familias de plantas. Esta plaga está matando árboles de arrayán, *Myrica cerifera* L., y de icaco, *Chrysobalanus icaco* L., dos plantas nativas y ornamentales valorizados en muchos lugares. El uso intensivo de insecticidas en áreas naturales y áreas residenciales infestadas es un método inapropiado de control por el gran número de plantas infestadas, el alto costo, y el daño posible a otros organismos que no son objetos de control. El control biológico es una solución muy necesitada para la escama lobulada de la laca. No se ha detectado parasitismo en la Florida. La escama lobulada de la laca es nativa de la India y Sri Lanka, ocurriendo en localidades al sur de los 16 grados de latitud norte. La variedad de hospederos conocidos incluye algunas de las mismas especies y familias de plantas hospederas que se encuentran en la Florida, más otros grupos de plantas que todavía no han sido detectados en la Florida. No se han buscados ni han estudiados los enemigos naturales de la escama lobulada de la laca, pero los de la escama verdadera de la laca de comercio, una escama relacionada, son relativamente bien conocidos, y algunos de ellos parecen tener un potencial para el control biológico de la escama lobulada de la laca. Los enemigos naturales más importantes son especies depredadoras lepidópteros y *Chrysopa*, y avispas chalcidoideos parasíticos de las familias Encyrtidae y Eulophidae. Las avispas chalcidoideos, con un alcance de hospederos más estrecho, parecen ser agentes potenciales de control biológico más apropiados. Entre estos, *Ta-*

chardiae (*tachardiae*) (Howard) (Encyrtidae), parece ser una especie particularmente prometedora. Ataca la escama lobulada de la laca, se conoce solamente de hospederos de escamas de la laca, no es hiperparasítico, es uno de los parasitoides más importantes de la escama de la laca, tiene 9-12 generaciones por año, y ocurre en las mismas condiciones climáticas como ocurre en el sur de la Florida. Se recomienda que se adquiera y se evalúe esta avispa y los dos otros parasitoides de la escama de la laca verdadera, *T. somervilli* Madhassen (Encyrtidae) y *Coccophagus tschirchii* Madhassen (Eulophidae), como agentes de control biológico potenciales de la escama lobulada de la laca. Se debe llevar a cabo exploraciones para enemigos naturales desconocidos de la escama lobulada de la laca en la India y Sri Lanka en localidades con un clima similar del sur de la Florida. Se aconseja hacer pruebas de especificidad de hospederos usando especies que pertenecen a los 12 familias de escamas (Coccoidea) nativas de la Florida y hemípteros relacionados para definir el alcance de hospederos potenciales y la seguridad de los candidatos de agentes de control biológico. Las perspectivas para el control biológico efectivo y seguro aparecen ser buenas. Ninguna de las escamas de la laca (Kerriidae) nativas se han encontrado ocurre en la Florida, y se conocen parasitoides que parecen ser especialistas restringidos y dañinos a sus hospederos de escamas de la laca.

Lobate Lac Scale Introduction, Impact and Potential Harm

The lobate lac scale, *Paratachardina lobata lobata* (Chamberlin), was first detected in southern Florida in 1999 (Hamon 2001), in Davie in Broward County (Division of Plant Industry [DPI], Florida Dept. of Agricultural and Consumer Services, collection record). During the spring and summer of 2002, the insect developed alarming densities on many host plants in Broward County. In a sample of a residential yard (0.33 acre = 0.135 hectare) in Ft. Lauderdale during August 2002, the scale was found to attack 55% (37/67) of the woody plant species present in 19 of 30 (63%) of the families (Pemberton, unpublished data). Preliminary surveys of natural areas in Broward and Miami-Dade Counties indicate high levels of attack on native plants. At Secret Woods Nature Center in Broward, the scale infests more than half of the tree and shrub species, and more than half of the individual plants examined (Pemberton, 2003). Many of the most important parks and preserves in southern Florida have been invaded, including: Everglades National Park, Big Cypress National Wildlife Refuge and Loxahatchee National Wildlife Refuge. Wax myrtle (*Myrica cerifera* L.), red bay (*Persea borbonia* (L.) Spreng.), coco plum (*Chrysobalanus icaco* L.), myrsine (*Rapanea punctata* (Lam.) Lundell), important ecological dominants of mesic habitats, and wild coffee (*Psychotria nervosa* Swartz), a dominant understory shrub in tropical hardwood hammock forest, are being killed in many localities. Coco plums and wax myrtles are important landscape plants in the region. Tropical fruits including avocado, grapefruit, mango, carambola (*Averrhoa carambola* L.), atemoya (*Annona cherimoya* Mill. × *A. squamosa* L.), sugar apple (*A. squamosa*), and other less important species are known hosts of the scale. Of these, carambola is the most severely damaged. Two of the most important inva-

sive weeds in southern Florida, melaleuca (*Melaleuca quinquenervia* S.T. Blake) and Brazilian pepper (*Schinus terebinthifolius* Haddi), are hosts of the scale, and the heavily infested large stands of melaleuca appear to generate large numbers of the pest which then infest other plants. Thus far, the scale has been found infesting more than 200 plant species in 55 families in south Florida (Hamon et al. 2002; Pemberton, unpublished data). Its negative effects will grow as it increases in abundance and spreads to new areas. The scale has also been recorded in the Bahamas (Hamon 2001). This insect could become a threat to cultivated and native vegetation in the West Indies and Mexico as well as the subtropical regions of Texas, California, and Hawaii.

Taxonomy and Identification

Specimens of a new lac scale found in southern Florida in 1999 were determined to be *Paratachardina lobata lobata* by Avas Hamon, Florida Division of Plant Industry (Hamon 2001) and confirmed by D. R. Miller, USDA-ARS-Systematic Entomology Laboratory. Many subsequent collections have been determined to be *P. lobata lobata*. This species first appeared in the literature in 1922, when E. E. Green published a detailed description and drawings of material from Sri Lanka. Green (1922) believed this insect to be conspecific with *Tachardia minuta* Morrison from the Philippines. Chamberlin (1923) recognized that the lobate scale from Sri Lanka was distinct and described it as the new species, *Tachardina lobata* (Chamberlin), based on a name used earlier by Green. The genus *Paratachardina* was separated from *Tachardia* by Balachowsky in 1950, but the new combination *Paratachardina lobata* was not published until 1976 (Varshney 1976a). The description of two subspecific taxa, *P. lobata* var. *schmidtii* (Madhassen) and *P. lobata* var. *walczychii* (Madhassen) from India by Madhi-

hassen (1946) resulted in a subspecific designation of *P. lobata lobata*. These subspecific separations were based primarily on differences in host plants from which the scales were collected, which is insufficient given the polyphagous nature of the species (R. K. Varshney, pers. comm.). Our Florida lobate lac scale appears to be similar to Green's drawings of the scale that became *P. lobata lobata*.

The lac scale family Kerridae is widely distributed in warmer parts of the New and Old World including Australia (Varshney 1976a). *Paratachardina* is in the subfamily Tachardininae with the genera *Afrotachardina* and *Tachardina*. The other subfamily in the family is the Tachardiinae, which contains *Austrotachardina*, *Kerria* (genus of the true lac scales), *Metatachardina*, *Tachardiella*, and *Austrotachardiella*. *Paratachardina* species are limited to the Old World, whereas *Austrotachardiella* and *Tachardella* (Tachardiinae) are the only New World genera in the family. Scales in the Tachardininae have horny testae, compared to testae composed of alcohol soluble resin in scales of the better known *Kerria* species and other members of the subfamily Tachardiinae. There are seven kerriid species in western United States, all in the genus *Tachardiella*, and a single *Austrotachardiella* species in Jamaica (Miller & Ben Dov 2002).

Native Range of the Lobate Lac Scale

The native range of the lobate lac scale, as defined in the literature, is Sri Lanka and the three southern states of India, below about 16 degrees north latitude. Recorded localities include the type localities of Peradeniya and Kandy in Sri Lanka, and Indian localities of Coimbatore in Tamil Nadu and Bangalore in Karnataka (Green 1922). Additional localities include Cuddapath in Andhra Pradesh (Ayyar 1930) and Calcutta in West Bengal (Varshney 1976a). The Calcutta locality, which is at nearly 23 degrees north latitude, is questionable because the scales from this collection were abnormal due to being parasitized which made their identification uncertain (R. K. Varshney, pers. comm.). Few specimens of the lobate lac scale exist in collections. The USNM has a single specimen, which is a paratype of Green's type material deposited at the University of California at Davis (D. R. Miller, pers. comm.). The Natural History Museum in London has no material (J. Martin, pers. comm.) and the scale is unlikely to be represented in Indian collections (Varshney, pers. comm.). I saw no material at the Indian Lac Scale Institute in Ranchi, Jarkhand during a September 2002 visit. A native distribution limited to southern India and Sri Lanka below 16 degrees north latitude is surprising given the scale's ability to thrive in southern Florida at about 26 degrees north latitude. Why it doesn't

occur farther north in India is unclear. Perhaps the limited collection records do not adequately define the native distribution.

Host Plants of Lobate Lac Scale in its Native Range

The lobate scale was described from material collected from *Flacourtia* (Flacourtiaceae) and *Fluggea* (Fabaceae) (Green 1922). The scale is known to be polyphagous and Varshney (1992) lists species in 42 genera of woody plants, in 25 families, as hosts, including: ***Annona***, *Aralia*, ***Acalypha***, ***Averrhoa***, ***Bauhinia***, *Cryptostegia*, ***Casuarina***, *Coffea*, *Celastrus*, ***Citrus***, ***Cestrum***, ***Dodonaea***, *Erythroxylum*, ***Ficus***, *Graptophyllum*, *Guazuma*, *Gymnosporia*, ***Hibiscus***, ***Hamelia***, *Kigelia*, *Loranthus*, ***Lagerstroemia***, ***Mangifera***, *Mallotus*, ***Michelia***, *Malpighia*, ***Pongamia***, *Pyrus*, *Punica*, *Phyllanthus*, *Semecarpus*, *Spondias*, *Stererospermum*, *Spathodea*, *Securinega*, *Sesbania*, *Santalum*, *Sterculia*, ***Terminalia***, and *Thespesia*. The genera in bold have been recorded as host species in southern Florida (Howard et al. 2002; Pemberton, unpublished data).

Need for Biological Control

Biological control offers a much needed solution to the lobate lac scale problem. No parasitism has been detected in the lobate lac scale populations in Florida. To attempt to detect parasitism, 3,000 mature female scales, collected on the twigs of 15 host plants (10 native plants and 5 non-native plants) in 7 localities (urban developed areas and nature preserves), were examined with a dissecting microscope for parasitoid emergence holes (Table 1). Three scales had possible parasitoid emergence holes. Dissections of these three scales found no evidence of parasitism (larval head capsules). During the process of examining and counting the 3,000 scales, large numbers of uncounted scales of various ages and sizes were scanned because the scales were in dense aggregations on the collected twigs. No emergence holes were noted in the uncounted scales.

Intensive use of insecticides to control this scale is problematic because of the cost to treat the large residential and natural areas infested, and the potential for environmental damage. Many scale insects have been successfully controlled by biological control, including the Florida red scale, *Chrysomphalus aonidum* (L.), formerly a pest in Florida (Kennett et al. 1999).

Recorded Predators of Lac scale, *Kerria lacca* (Kerr) in India

Little is known about the predators of lobate lac scale. By contrast, the predators and other natural enemies of commercial lac scale, *Kerria lacca* (Kerr) in India are better known, and the

TABLE 1. EXAMINATION OF LOBATE LAC SCALES FOR PARASITISM-PARASITOID EMERGENCE HOLES

Collection Locality	Host plant N = Florida native	Date collected	No. examined	Holes?
Tree Island Weston, Broward Co. (preserve)	<i>Persea borbonia</i> (L.) Spreng. N	10 Oct. 2002	200	none
	<i>Rapanea punctata</i> (Lam.) Lundell N	10 Oct. 2002	200	none
Ft. Lauderdale, Broward Co. (residential area)	<i>Myrica cerifera</i> L. N	10 Oct. 2002	200	none
	<i>Quercus laurifolia</i> Michx. N	10 Oct. 2002	200	none
	<i>Psychotria nervosa</i> Swartz N	11 Oct. 2002	100	none
	<i>Chrysobalanus icaco</i> L. N	11 Oct. 2002	100	none
Secret Woods, Broward Co. (preserve)	<i>Ficus aurea</i> Nutt. N	21 Oct. 2002	100	none
	<i>Baccharis glomeruliflora</i> Pers. N	21 Oct. 2002	100	none
	<i>Persea borbonia</i> N	21 Oct. 2002	100	none
	<i>Chrysobalanus icaco</i> N	21 Oct. 2002	100	none
	<i>Rapanea punctata</i> N	21 Oct. 2002	100	none
Plantation, Broward Co. (business park)	<i>Eugenia axyridis</i> (Swartz) Willd. N	21 Oct. 2002	100	none
	<i>Quercus laurifolia</i> N	22 Oct. 2002	100	3? ¹
	<i>Calophyllum antillanum</i> Britt.	22 Oct. 2002	100	none
Heritage Park, Broward Co. (city park)	<i>Bursera simaruba</i> (L.) Sarg. N	22 Oct. 2002	100	none
	<i>Mangifera indica</i> L. N	22 Oct. 2002	100	none
	<i>Ficus elastica</i> Hornem.	22 Oct. 2002	100	none
	<i>Bucida buceras</i> L.	22 Oct. 2002	100	none
Everglades NP, Dade Co. (preserve)	<i>Eugenia luschnathiana</i> O. Berg.	22 Oct. 2002	100	none
	<i>Persea borbonia</i> N	27 Oct. 2002	100	none
	<i>Chrysobalanus icaco</i> N	27 Oct. 2002	100	none
Big Cypress NWR, Collier Co. (preserve)	<i>Rapanea punctata</i> N	27 Oct. 2002	100	none
	<i>Salix caroliniana</i> Michx. N	27 Oct. 2002	100	none
	<i>Chrysobalanus icaco</i> N	27 Oct. 2002	100	none
	<i>Ficus aurea</i> N	27 Oct. 2002	100	none
Total	<i>Myrica cerifera</i> N	27 Oct. 2002	100	none
			3000	3? ¹

¹Dissection of the three scales with holes found no evidence of parasitism such as larval head capsules.

most important species are relatively well studied. The most important invertebrate predators of the commercial *K. lacca* are predatory Lepidoptera (primarily *Eulema amabilis* Moore (Noctuidae) and *Pseudohypatopa* (= *Holcocera pulvera* Meyr; (Blastobasidae), followed by lacewings (*Chrysopa* spp., Chrysopidae: Neuroptera) (Narayanan 1962). The predators causing the greatest mortality of *K. lacca* are *E. amabilis* and *P. pulvera*, which can destroy 35-40% of a lac crop (Malhotra & Katiyar 1975 cited by Sharma & Jaiswal 2002). Their larvae feed on the scales from silken tubes and consume between 40 and 60 scales during their development. The *Chrysopa* spp. are sporadic pests that sometimes cause significant mortality (Sharma & Jaiswal 2002). The important predators of *K. lacca* are thought not to be limited to lac scales in their range of prey (Sharma & Bhattacharya, pers. comm.). Less important predators include many moths and lacewings (Narayanan 1962), a cucujid, a tenebrionid, a mycetophagid, several blattellids (Bhattacharya 2002), as well as an assortment of coccinellids and other insects (Sharma et al., unpublished data). Coccinellids may be worth investigating because many species are scale specialists (Hodek 1973).

The earliest and perhaps best known example of insect biological control involved the vedalia beetle, *Rodolia cardinalis* (Mulsant) on the cottony cushion scale (*Icerya purchasi* Maskell) in California during the late 1800s (DeBach 1974). A scale-feeding coccinellid (*Cryptognatha nodiceps* Marshall) successfully controlled the coconut scale (*Aspidiotus destructor* Signoret) in Fiji (Sweetman 1936), but coccinellids can have difficulty in successfully controlling some scales with hard coverings, such as many Diaspididae (Clausen 1940). This suggests that coccinellids might have difficulty controlling the lobate lac scale which has a very hard testa.

Recorded Parasitoids of Lac Scales (Kerriidae)

Varshney (1976b) lists and discusses 28 parasitoids recorded from lac scale species worldwide. The four braconid wasps listed are erroneously recorded as lac scale parasitoids and are actually parasitoids of some of the many predacious Lepidoptera that attack lac scales (Editor V. K. Gupta's note in Varshney 1976b). The remaining 24 species are all chalcidoid wasps (Aphelinidae, Encyrtidae, Eulophidae, Eupelmidae and Pteromalidae). Most

(16) of these have been recorded from the commercial lac scale in India. The nine parasitoids which regularly attack the commercial lac scale (Narayanan 1962) are listed in Table 2.

The parasitoids of lobate lac scale have not been sought nor studied, but three species, *Tachardiaephagus tachardiae* Howard (Encyrtidae), *Tetrastichus purpureus* Cameron (Eulophidae), and *Marietta leopardina* Nietner (Aphelinidae), are reported to attack it (Varshney 1976b). *Tetrastichus purpureus* is a primary parasitoid of lac scales and a hyperparasitoid of chalcidoid primary parasitoids of lac scales. *Marietta leopardina* also is probably a hyperparasitoid of chalcidoids attacking lac scale, as is another parasitoid, *Marietta javensis* Howard, commonly reared from commercial lac (Narayanan 1962). Riek (1970) observed that *Marietta* species are hyperparasitoids. *Tachardiaephagus tachardiae* and two other parasitoids commonly associated with the commercial lac scale, *Tachardiaephagus somervilli* Madhiahassen (Encyrtidae) and *Coccophagus tschirchii* Madhiahassen (Eulophidae), are not known to be hyperparasitoids nor have alternative hosts (Narayanan 1962). The latter two species also may have the ability to parasitize the lobate lac scale.

Parasitoid Biology, Abundance, and Impact on Commercial Lac Scale in India

Lac scale parasitoids are well adapted to their hard-bodied hosts. The wasps lay one or more eggs through the anal tubercular opening on top of the testa, and either oviposit on or in the body

of the scale, depending on the parasitoid species (Narayanan 1962). Superparasitism can occur but typically one parasitoid larva occurs in a single scale (Narayanan 1962). The parasitoids have life cycles of about one month in length, compared to 4-9 months, depending on the scale strain and season, for *K. lacca* (Narayanan 1962). The parasitoids can therefore have many generations within a particular scale colony, attacking older stages as the scale colony matures.

Of the regularly occurring parasitoids, *Tachardiaephagus tachardiae* and *Tetrastichus purpureus* are the most abundant (Bhattacharya 2002). *Tachardiaephagus tachardiae*, *Tetrastichus purpureus*, and *C. tschirchii* have 10-12 generations on commercial lac each year, compared to 9 generations for *Paraechthrodryinus clavicornis* Cameron, an encyrtid that can be either a primary or secondary parasitoid (Narayanan 1962). The level of parasitism, measured for the regularly occurring parasitoid complex for seven years from 1928 to 1935, was only 4.8%, but in certain localities and seasons the parasitism level could be as high as 50% (Narayanan 1962). Chauhan (1984 cited in Sharma & Jaiswal 2002) reinterpreted these data and reported that parasitism of the relatively more important females was between 20-37%. Parasitized scales are consumed in large numbers by predatory Lepidoptera larvae, primarily *E. amabilis* and *H. pulvera*, which are the major pests of lac scale culture. After cultural methods were developed to reduce the abundance of these lac scale predators, the average parasitism level jumped to about 30% (Bhatta-

TABLE 2. MOST IMPORTANT PARASITOIDS OF LAC SCALE, *KERRIA LACCA* IN INDIA (NARAYANAN 1962 AND VARSHNEY 1976B). SPECIES IN BOLD ARE KNOWN TO PARASITIZE THE LOBATE LAC SCALE.

Parasitoid families and species	Alternate hosts	Hyperparasitoid?	Comments
Eulophidae			
<i>Coccophagus tschirchii</i> Madhiahassen	<i>Kerria</i>	no	
<i>Marietta javensis</i> Howard	<i>Aspidiotus</i> (Diaspididae)	yes, of chalcidoids of <i>K. lacca</i>	chiefly on males
<i>Marietta leopardina</i> Nietner		probably	
<i>Tetrastichus purpureus</i> Cameron	<i>Aspidiotus</i> (Diaspididae) <i>Chionaspis</i> (Diaspididae)	yes, of <i>C. tschirchii</i> and <i>T. tachardiae</i>	primary and secondary parasitoid
Encyrtidae			
<i>Erencyrtus dewitzi</i> Madhiahassen	<i>Kerria</i> , <i>Metatachardia conchiferata</i> (Green)	no	chiefly on 4th instar females
<i>Eupelmus tachardiae</i> Howard	<i>Machaerota</i> (Machaerotidae)	yes, of <i>Microbracon</i> and <i>Apanteles</i>	primary and secondary parasitoid
<i>Paraechthrodryinus clavicornis</i> Cameron	<i>Kerria</i>	yes, of chalcidoids of <i>K. lacca</i>	
<i>Tachardiaephagus tachardiae</i> Howard	<i>Kerria</i>	no	
<i>Tachardiaephagus somervilli</i> Madhiahassen	<i>Kerria</i>	no	

charya, pers. comm.). This level occurs despite the abundant and persistent hyperparasitoids which presumably kill many primary parasitoids.

Recorded Pathogens of Commercial Lac Scale in India

Sharma & Jaiswal (2002) reviewed the literature on diseases of lac scale. Most of the organisms involved are fungi and these are primarily black molds, such as species of *Capnodium*, *Fumago*, and other species that grow on the honeydew secreted by the scales. These fungi can cause losses in lac yield because their growth inhibits the respiration, mating, larval emergence, and efficient use of the plant by the scale. A *Pythium* sp. is reported to cause heavy mortality of the larvae, which fail to complete development (Misra 1928 cited in Sharma & Jaiswal 2002).

Biological Control Approaches for the Lobate Lac Scale

Several biological control approaches to acquire natural enemies appear feasible. Because the natural enemies of lobate lac scale have been neither sought nor studied, explorations for its natural enemies should be made in its native range. The Biological Control Institute in Bangalore has expressed a willingness to provide assistance in such a research project (J. Rabindra, pers. comm.). Bangalore is a locality where the lobate lac scale has been collected so would be a good base to conduct surveys. It is not known how common the lobate lac scale is within its native range. Green (1922) indicated that he had known the species for more than 20 years, suggesting that it might be common at least in parts of Sri Lanka. For this reason, surveys should be made in Sri Lanka as well as in southern India. Baiting for parasitoids and other natural enemies, with scale cultures of a range of age-size classes, in lobate lac scale's native range could be informative and profitable, especially if the lobate lac scale is uncommon or has a patchy distribution.

Another approach would be to examine the potential of using parasitoids of commercial lac scale for the control of lobate lac scale. Some, including *Tachardiaephagus tachardiae*, are known to attack lobate lac scale and others may have the potential to use the scale. In September 2002, I visited the Indian Lac Institute in Ranchi, Jarkhand, India, and R. K. Varshney in Aligarh, Uttar Pradesh, India, to investigate the possibilities of using the parasitoids of the commercial lac scale for the biological control of lobate lac scale. The Indian Lac Institute was established in 1926 to conduct research on lac scale cultivation and lac scale products which include resin, waxes, dyes and other chemicals. Lac cultivation is an ancient agricultural activity and cottage industry in India, that was mentioned in the Hindu Vedas more than 2,000 years ago (Mukhopadhyay & Muthana

1962). Income from lac is an important subsidiary income for farmers and forest-dwelling peoples in Bihar, Jarkhand, Orissa and other areas of India (Mukhopadhyay & Muthana 1962).

Scientists at the Indian Lac Institute are intimately familiar with lac scale cultivation and maintain lac scale cultures for research purposes, including research on the pests of lac scale. They have the capability to collect desired parasitoids that emerge from their cultures and ship them to a Florida quarantine laboratory. Adults of lac scale parasitoids are apparently short-lived (A. Bhattacharya, pers. comm.) but, if fed with honey, they might live long enough to be successfully shipped to Florida. The Lac Institute also has the capability to provide lac scale parasitized with desired parasitoid species. To do this, they could rear parasitoids of interest from their lac scale cultures, and induce these to parasitize clean (unexposed) even-aged cultures of the lac scale. The parasitized lac scale could be protected from additional parasitism by unwanted species and maintained for several weeks to allow for parasitoid development, and then shipped to Florida quarantine prior to adult parasitoid emergence. Because the temporal life cycles of lac scale strains are well known, it would be possible to induce parasitism in cultures of large recently mated female scales that are months away from producing crawlers. After parasitoid emergence and transfer to lobate lac scale cultures in the Florida quarantine laboratory, the lac scale hosts could be destroyed prior to crawler emergence. Advantages of obtaining parasitoids from lac scale cultures at the Lac Institute would include the following: (a.) known, desired parasitoid species could be obtained in sufficient numbers; (b.) these should have few if any hyperparasitoids; and (c.) the potential risk related to large numbers of small crawlers associated with the commercial lac hosts could be avoided. Because the lac scale is quite polyphagous (Varshney 1992), its regularly occurring parasitoids probably have the ability to locate the scale on very diverse host plants. This behavioral trait should give these parasitoids the ability to locate lobate lac scale on its diverse plant hosts in Florida. *Tachardiaephagus tachardiae* is the parasitoid of most interest because it is known to be able to attack the lobate lac scale. Two other parasitoids, *Tachardiaephagus somervilli* and *C. tschirchii*, should be tested as well. They are not recorded to parasitize lobate lac scale, but the absence of recorded parasitism may reflect the lack of parasitoid rearing on the lobate lac scale. Most of the research on lac scale predators and parasitoids has been done north of the apparent native range of the lobate lac scale in India. The commonness of these parasitoids, despite the presence of predators and hyperparasitoids, suggests the capacity to develop large populations when freed of these enemies. This could make them valuable in

lobate lac scale control in Florida. These parasitoids should also be able to establish and thrive in the climatic conditions of southern Florida because the climates of Ranchi, Jarkhand and southern Florida are similar. Ranchi is located at 24 degrees N. latitude and 600 meters above sea level, compared to Miami at 26 degrees N. near sea level. Both areas have cool dry winters, hot rainy summers, and infrequent frosts.

Safety Considerations of Lobate Lac Scale Biological Control

The adoption of nontarget native insects by introduced biological control insects has been increasingly documented in recent times (Louda et al. 2003). The potential host range of candidate biological control insects should be predicted prior to their release to lessen the risk to native insects and introduced insects of value (Strong & Pemberton 2000). This can be accomplished by an evaluation of the well-known taxonomically limited prey specialization of some natural enemy taxa, and host-specificity testing research. Host-specificity testing of parasitoids has been shown to be a good predictor of field host range (Barratt et al. 2000) and is recommended for candidate biological control agents of the lobate lac scale. Risk to nontarget insects depends on how closely related the potentially exposed, valued insect fauna is to the lobate lac scale, and the degree of specificity of the natural enemies employed against the lobate lac scale. There are no native species of the lac scale family (Kerriidae) in Florida and, as mentioned above, only seven kerriids occur in the United States and these are confined to the arid Southwest which would probably preclude both exposure and adoption by parasitoids introduced to Florida. Neither the genus *Paratachardina* nor the subfamily to which it belongs (the Tachardinae) occur in the New World (Varshney 1976a), so there are no closely related scales in the region. The closest family members are *Tachardiella* species in Texas and Mexico and a single *Austrotachardiella* species in Jamaica (Miller & Ben Dov 2002). Testing of some species in these genera should be considered, although obtaining and/or culturing them could be difficult. Representative species of the 13 native scale families (superfamily Coccoidea) in Florida also should be tested. These families are the Acleridae, Asterolecaniidae, Cerococcidae, Coccidae, Conchaspidae, Dactylopididae, Diaspididae, Eriococcidae, Kermesidae, Lecanodiaspididae, Margarodidae, Ortheziidae, and Pseudococcidae (derived from Miller and Ben Dov in 2002 by F. W. Howard). The inadvertent reduction of native scale populations by introduced natural enemies might have consequences far beyond the scales affected. *Dactylopius* scales illustrate the point. *Dactylopius* species have been successfully used in many parts of the world to

control exotic weedy prickly pear cacti (*Opuntia* species) (Julien & Griffiths 1998). This suggests that *Dactylopius* species play a role in regulating their host *Opuntia* in their native areas, such as in Florida. Reduction of *Dactylopius* scales could reduce or eliminate their regulatory effects, which could allow some host *Opuntia* species to become unnaturally abundant. One Florida species, *Opuntia stricta* (Haworth) Haworth, has been a severe weed in many parts of the world (Julien & Griffiths 1998), where it has been introduced and without its natural enemies. Representatives of other hemipteran families, particularly those that have species with sessile or sedentary nymphs, should be tested. This includes: the recently introduced psyllid *Boreioglycaspis melaluciae* Moore, a promising biological control agent of *Melaleuca quinquenervia* (Cav.) S.T. Blake; *Calophya* spp. (Psyllidae) Similarly Hemiptera being evaluated as potential biological control agents of Brazilian pepper and strawberry guava (*Psidium cattleianum* Sabine) in Florida should be tested. These include and *Tectococcus ovatus* Hempel (Eriococcidae) respectively (J. P. Cuda, pers. comm.). Although it is desirable to avoid nontarget use of native insects, the potential adoption of some native insects as hosts should not in my opinion automatically exclude the introduction of a promising natural enemy. The potential risk to native and valued insects needs to be evaluated in relation to the potential benefit gained by control of lobate lac scale, which is a great threat to native and economic vegetation in Florida and elsewhere where it is likely to spread. It should be possible, however, to find and employ natural enemies with narrow enough host ranges to minimize the risk to nontarget species. Parasitoids will probably be safer agents than predators.

A cooperative biological control effort against the lobate lac has been developed. Participants at this point include this author, R. W. Pemberton (USDA-ARS), R. Nguyen (Division of Plant Industry, Bureau of Methods and Biological Control, Gainesville, Florida), F. W. Howard (University of Florida, IFAS, Davie), Florida, and Indian cooperators at the Indian Lac Institute and Biological Control Institute in Bangalore.

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A NEW GENUS OF TROPIDUCHIDAE (HEMIPTERA: FULGOROIDEA) FROM CHINA AND VIETNAM, WITH DESCRIPTION OF EGGS

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ABSTRACT

Paricanoides Liang gen. nov. (Hemiptera: Fulgoroidea: Tropicuchidae) is described to include two new species, *Paricanoides orientalis* Liang sp. nov. (type species, south China: Hainan Island and north Vietnam: Tonkin, Blao) and *Paricanoides dalatensis* Liang sp. nov. (Vietnam: Dalat). Male genitalia of the new species are illustrated and a dorsal habitus is provided for the male of *P. orientalis*. The eggs of *P. dalatensis* are described and illustrated with scanning electron micrographs. The new genus *Paricanoides* is distinguished by its forewing venation and is tentatively placed in the tribe Paricanini Melichar.

Key Words: *Paricanoides*, new species, SEM

RESUMEN

Paricanoides Liang gen. nov. (Hemiptera: Fulgoroidea: Tropicuchidae) esta descrita para incluir dos nuevas especies, *Paricanoides orientalis* Liang sp. nov. (la especie tipo, del sur de China: Isla de Hainan y de Vietnam del Norte: Tonkin, Blao) y *Paricanoides dalatensis* Liang sp. nov. (Vietnam: Dalat). Se ilustra los genitales de los machos de las nuevas especies y el dorso del macho de *P. orientalis*. Se describe e ilustra los huevos de *P. dalatensis* con micrográficos del microscopio electrónico (SEM). Se distingue el nuevo género *Paricanoides* por las venas del ala anterior y esta puesta tentativamente en el tribu Paricanini Melichar.

The Tropicuchidae is one of the smaller families of the planthopper superfamily Fulgoroidea, currently containing about 380 described species in over 110 genera (Metcalf 1954; Fletcher & Carver 1991; Yang et al. 1989). Members of the family can be separated from other planthoppers by the presence of a groove or a fine line separating the apex of the mesonotum from the rest of the mesonotal disc (O'Brien & Wilson 1985).

Species of Tropicuchidae are found in all warm temperate and tropical regions of the world associated with herbaceous and woody dicotyledons, palms, grasses, rushes and ferns, and have adapted themselves to habitats ranging from rain-forest to macchia and semi-desert (Fennah 1982). Both nymphs and adults feed above ground on their hosts, in most cases woody dicotyledons, and monocotyledons (primarily Poaceae and Arecaceae) (Wilson et al. 1999). Sixteen tropiduchid species were recorded as pests of 10 plants (Wilson & O'Brien 1985). *Numicia viridis* Muir is an important pest of sugarcane in southern Africa (Fennah 1969; Carnegie 1980). *Ommatissus lybicus* Bergevin, the 'Dubas bug', is a serious pest of date palm (*Phoenix dactylifera*) in the Middle East and North Africa (Hussain 1963; Asche & Wilson 1989).

The tropiduchid faunas of China, Indochina and southeast Asia remain inadequately studied and there is still much basic taxonomic work to be done on the group in these regions. While sorting and identifying Oriental Tropicuchidae from ma-

terial in the Insect Collection of the Institute of Zoology, Chinese Academy of Sciences, Beijing, China and elsewhere, I found two undescribed species with very distinct forewing venation which could not be placed in any known genus. Specimens of the two species were collected from south China (Hainan Island) and Vietnam (Tonkin, Blao, Dalat). In addition, an unidentified female specimen, collected at Kalabakan, Borneo, was found in the Bernice P. Bishop Museum, Honolulu, Hawaii, USA. In the present paper, I describe and illustrate the new genus *Paricanoides* Liang gen. nov. and its two included new species *Paricanoides orientalis* Liang sp. nov. (type species) from south China (Hainan Island) and north Vietnam (Tonkin) and *Paricanoides dalatensis* Liang sp. nov. from Vietnam (Dalat). The new genus is tentatively placed in the tribe Paricanini Melichar. I also present a brief description of the eggs of *Paricanoides dalatensis* plus scanning electron micrographs, as ontogenetic stages in tropiduchids and other fulgoromorphans are largely unresearched.

MATERIALS AND METHODS

The specimens studied in the course of this work were from the Bernice P. Bishop Museum, Honolulu, Hawaii, USA (BPBM); the Insect Collection of the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IZCAS) and the

Department of Biology Insect Collection, Nankai University, Tianjin, China (NU).

Eggs were obtained for scanning electron microscopy (SEM) by dissecting the dry, pinned museum specimens. They and the female genitalia were mounted on aluminum stubs with double-sided sticky tape and coated with gold-palladium using a sputter coater. Observations were made with a JEOL JSM-6301F (Japanese Electronic and Optical Ltd., Tokyo, Japan) scanning electron microscope, operated at accelerating voltages of 15 kV.

Morphological terminology follows that of Kramer (1950) and Fennah (1982).

DESCRIPTIVE TAXONOMY

Paricanoides Liang gen. nov.

Type species: *Paricanoides orientalis* Liang sp. nov.

Description. Medium sized, somewhat stout tropiduchids (Figs. 1-4), length (from apex of vertex to tip of forewings) 12.8-14.0 mm. General color pale green, frons usually with an inverse U-shaped, reddish stripe (Figs. 16, 27); anterior, posterior and lateral margins of vertex and carinae on pronotum and mesonotum, usually reddish; forewings transparent, veins brown, apex usually suffused with brown (Figs. 1-4, 17).

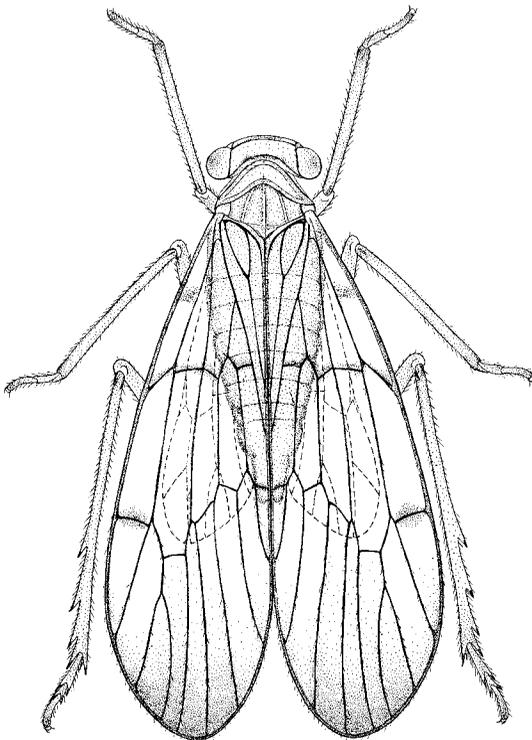
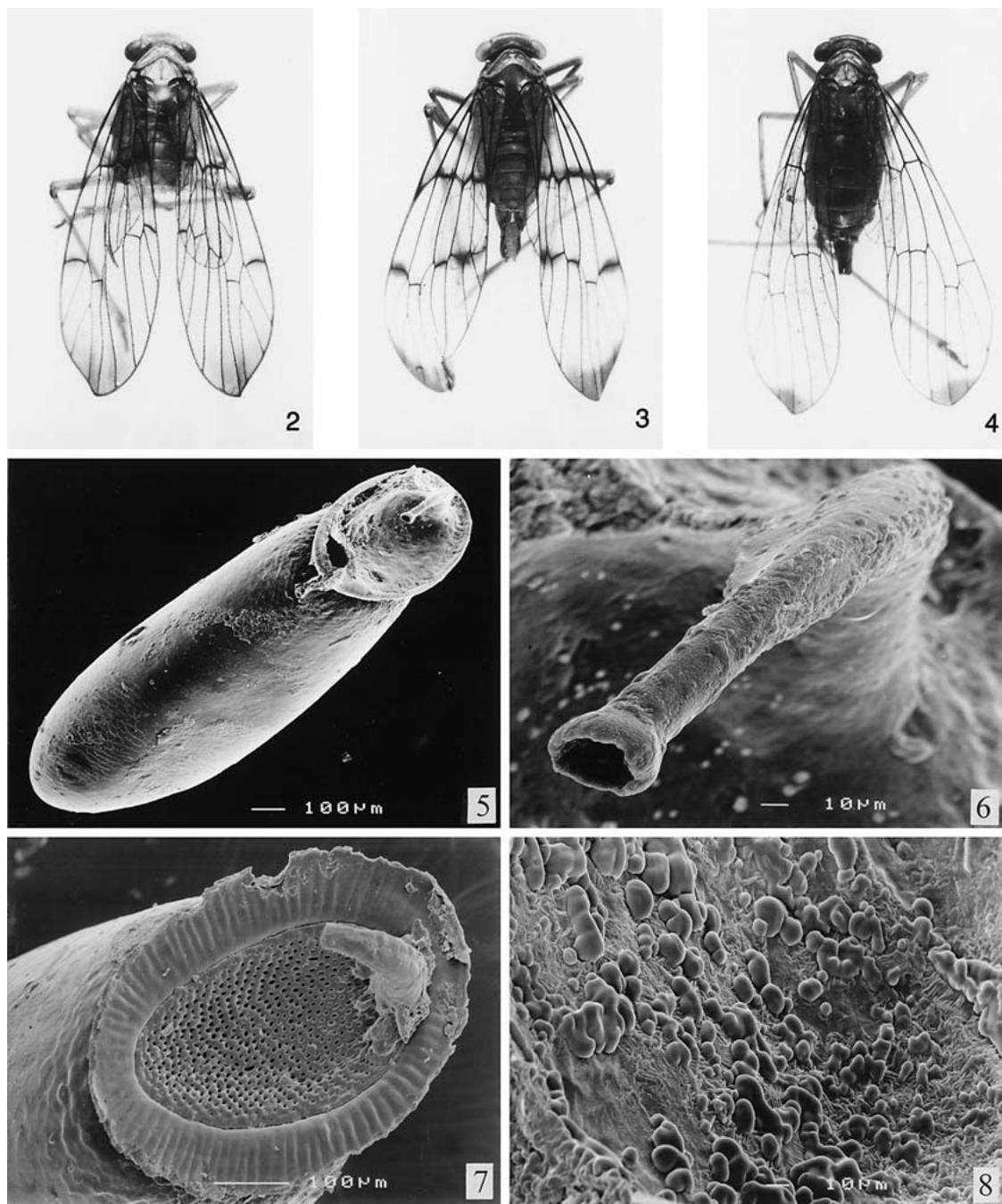


Fig. 1. *Paricanoides orientalis* Liang sp. nov. (China: Hainan Island, IZCAS): male paratype, dorsal habitus.

Head (Figs. 1-4, 15, 26) short and broad in dorsal view, distinctly broader than anterior part of pronotum; vertex shorter than pronotum in middle line, without median longitudinal carina (very fine carina present in *Paricanoides dalatensis* Liang sp. nov.), anterior margin not carinate, broadly arched or nearly straight, posterior margin finely carinate and arched anteriorly, lateral margins slightly carinate and converging anteriorly. Frons (Figs. 16, 27) broad and elongate, somewhat subquadrate, slightly longer than wide, basal part slightly wider than distal part in ventral view, surface smooth, without median carina (thickened median carina present in the unidentified female specimen collected from Borneo at BPBM), lateral margins not carinate. Postclypeus shorter than frons, relatively broad, smooth, without median carina, lateral margins not carinate. Anteclypeus narrow, without median and lateral carinae. Eyes oval. Ocelli two, small. Antennae with scape very short and small, ring-like; pedicel subglobose, short and small, covered with long setulae and about 15-20 disc-like sensory plaque organs, both setulae and sensory plaque organs extending to base of pedicel. Rostrum short, extending between trochanters of fore legs, apical segment short, longer than wide, slightly longer than 1/2 length of subapical segment. Pronotum (Figs. 15, 26) shorter than mesonotum in middle line, narrow anteriorly and broad posteriorly, disc relatively broad, strongly arched anteriorly, lateral marginal areas strongly curved down and nearly vertical, sublateral carinae broad, without median carina (very faint carina present in *Paricanoides dalatensis*), posterior margin angulately excavate with posterior marginal area broadly elevated and anteriorly sloping. Mesonotum (Figs. 15, 26) tricarinate on disc. Forewings (Figs. 1-4, 17) coriaceous, transparent, base relatively narrow, broad subapically; corium smooth, without granulation, costal marginal area without transverse veinlets; veins prominent and thickly covered with short setae dorsally and ventrally (veins in basal corial area not covered with setae dorsally); venation as in Figure 17, R branched apically, P and Cu forked much basally with cell PCu very short and small, Cu1 branched much basally; with 2 rows of transverse veinlets, one at basal 1/3 and the other at apical 1/3, enclosing 5 elongate cells in middle and 7-9 cells apically (11 apical cells in the unidentified female specimen collected from Borneo at BPBM), with 4 basal cells in corium before the first transverse veinlets. Hindwings (Figs. 1, 2) much smaller and shorter than forewings, about 0.4-0.6 times length of forewings, not extending beyond apex of ovipositor in females, veins prominent, thickly covered with short setae dorsally and ventrally, venation as in Figure 18. Legs elongate, hind tibiae with 3 lateral spines beyond middle and 6 apical black-tipped spines, metatar-

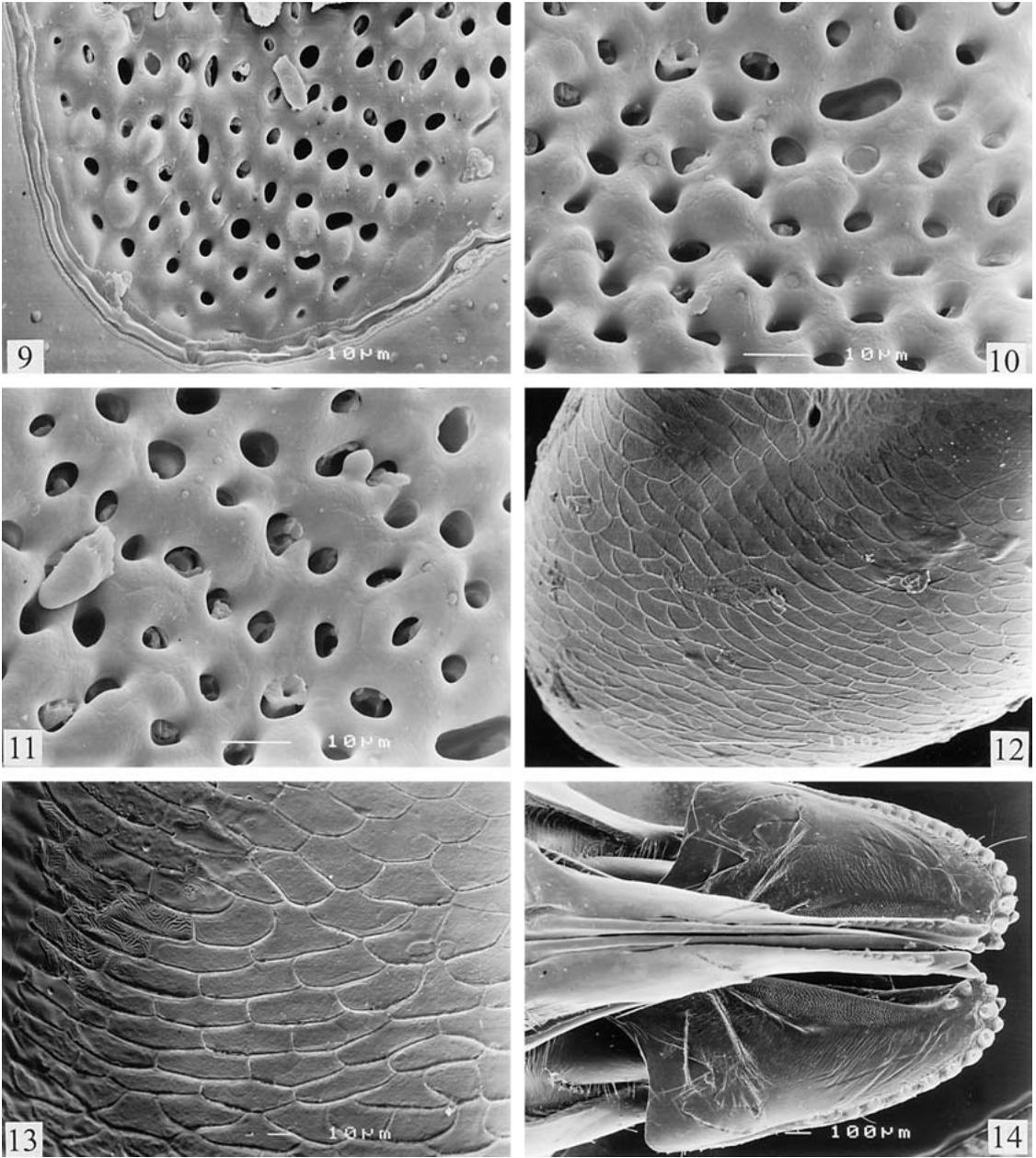


Figs. 2-8. *Paricanoides* species. 2-4. Dorsal habitus of *P. orientalis* Liang sp. nov. 2. male holotype (China: Hainan Island, IZCAS); 3. male paratype (Vietnam: Tonkin, IZCAS); 4. a female of non-type series (Vietnam: Blao (Balao)); 5-18. Scanning electron micrographs of eggs of *P. datensis* Liang sp. nov. 5. whole egg, dorsolateral view; 6. micropylar horn, dorsal view; 7. operculum, dorsal view; 8. waxy secretion on operculum.

sal segments I and II with 6-8 and 2 black-tipped spines apically, respectively.

Male genitalia (Figs. 19-25, 28-33) with pygofer narrow and high in lateral view, dorsal posterior margin angulately produced posteriorly,

dorsal margin strongly excavated to accommodate anal tube, ventral margin strongly excavated anteriorly to accommodate parameres in ventral view. Anal tube very elongate and slender, anal style relatively short and small. Parameres



Figs. 9-14. *Paricanoides* species. 9-11. respiratory pores on operculum; 12, 13. chorion surface; 14. female genitalia, ventral view, showing teeth of third valvula of ovipositor.

relatively large and broad, with apex somewhat roundly produced posteriorly in lateral view, upper margin with apex angulate or acute, with a lateroventrally directed process beyond the angulate or acute apex and a small dorsally directed process near middle. Aedeagus robust, asymmetrical; perianthrium well developed, asymmetrical, surrounding penis at base, distally attached to penis ventrally, with an anterodorsally or poster-

odorsally directed process in middle at left side, apex with two dorsally directed processes or truncate at left side and having an apical, anterodorsally directed process at right side; penis with one apical, dorsally or anterodorsally directed process at left side and a subapical, branched process at right side.

Female genitalia with third valvula having 15-17 visible, short, stout teeth apically (18 teeth in

the unidentified female specimen collected from Borneo at BPBM), and 1 outer tooth apically (Fig. 14).

Etymology. Named for its similarity of appearance to *Paricana* Walker 1857. Gender: feminine. *Included species and distribution.* Two new species and one unidentified species currently known only from one female specimen which was collected at Kalabakan, Borneo and is deposited in BPBM; south China (Hainan Island), Vietnam (Tonkin; Dalat), and Borneo.

Remarks. The new genus can be easily distinguished from other known Oriental tropiduchid genera by the combination of the following characters: head short and broad, vertex with anterior, posterior and lateral margins not distinctly carinate, without median carina; frons broad and smooth, usually with an inverse U-shaped reddish stripe, lateral margins not carinate, without median carina (thickened median carina present in one unidentified female specimen collected from Borneo at BPBM); forewings with P and Cu forked extremely basally and cell PCu very small, with two rows of cross-veins at basal 1/3 and apical 1/3, respectively, enclosing 5 elongate cells in middle and 7-11 apical cells (Figs. 1-4, 17); hind tibiae with 3 lateral spines beyond middle; and the male genitalic structure (Figs. 19-25, 28-33). The forewing venation of the new genus appears very unusual and distinct within Tropicuchidae (Figs. 1-4, 17; see also Fennah 1982: Figs. 1-26, 35, 36).

Fennah (1982) revised the higher classification of the Tropicuchidae and recognized 15 tribes in the family: Alcestini, Catulliini, Cixiopsini, Cyphoceratopini, Eporini, Eutropistini, Isporisini, Neommatissini, Paricanini, Remosini, Tambiniini, Tangiini, Tropicuchini, Trypetimorphini and Turneriolini. More recently, Szwedo (2000) established the sixteenth tribe, Jantaritambiini, based on a fossil species *Jantaritambia serafini* Szwedo, described from Eocene Baltic amber. The tribal system of Fennah (1982) is considered purely phenetic rather than phylogenetic since it was primarily based on diagnostic characters without any discussion of homology and evolutionary trends (Asche & Wilson 1989). Monophylies of these tribes and their included genera and the relationships among the genera and tribes have yet to be tested cladistically (Asche & Wilson 1989; Szwedo 2000; Liang & Jiang 2003).

I tentatively place *Paricanoides* in the tribe Paricanini Melichar, mainly based on the forewing venation, the shape of head and antennae and the number of the lateral spines on hind tibiae. Paricanini, as defined by Fennah (1982), includes only 3 genera, *Paricana* Walker 1857 (Borneo, Sumatra, Malay Peninsula, Japan; Bonin Island), *Leusaba* Walker 1857 (Borneo, Philippines, Sri Lanka) and *Stacota* Stål 1859 (Philippines, Sri Lanka), all from the Oriental region. *Paricanoides* can be distinguished from *Paricana* by the forewings with few

apical and subapical cells, P and Cu forked more basally and cell PCu much shorter and smaller, two rows of cross-veins located at basal 1/3 and apical 1/3, respectively; and hind tibiae with 3 lateral spines beyond middle (see Walker 1857). It can be distinguished from *Leusaba* by the frons and postclypeus without median carina, forewings with few apical and subapical cells, and hindwings with few apical cells (see Walker 1857; Distant 1906). It can be separated from *Stacota* by the very short head, distinctly shorter than broad; frons broad, subquadrate; vertex and frons not carinate laterally and without median carina; and forewings without transverse veinlets on costal cell (see Stål 1859; Distant 1906).

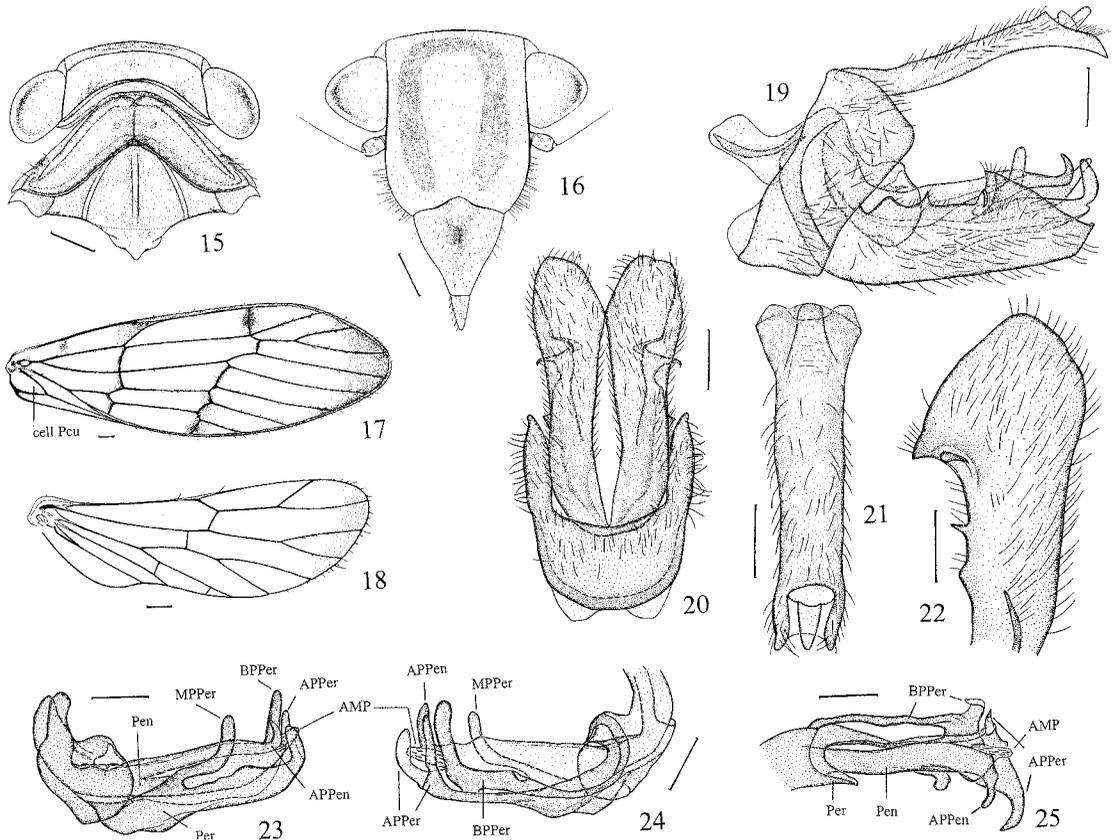
Based on the shape of antennae and the number of lateral spines on hind tibiae, *Paricanoides* is similar to members of the Isporisini (Oriental) but its head morphology and forewing venation indicate that it belongs in the Paricanini. *Paricanoides* differs from members of the Isporisini in the head distinctly short and broad, frons with lateral margins not elevated and lacking median carina, and the forewings with the cell PCu very short and small. *Paricanoides* is also similar to *Pseudoparicana* Melichar 1914 (Tropicuchini) from New Guinea in forewing venation but differs from the latter in the vertex not carinate medially, hind tibiae with 3 lateral spines, and the forewing with the first transverse veinlets much more basal.

Paricanoides orientalis Liang sp. nov.

(Figs. 1-4, 15-25)

Description. Length (from apex of vertex to tip of forewings): ♂ 12.8-13.8 mm; ♀ 13.8 mm. Body length (from apex of vertex to tip of anal tube): ♀ 9.3 mm. Forewing length: ♂ 11.0-12.0 mm; ♀ 12.0 mm.

General color pale greenish or greenish stramineous, probably green in life; frons greenish, with an inverse U-shaped, reddish stripe (Fig. 16); antennal pedicel and ocelli pale reddish; vertex with hind carinate margin with two brown suffusion areas laterally; pronotum with broadly elevated anterior and posterior margins and carinae on mesonotum pale reddish or reddish ochraceous; a transverse band on lateral, ventrally curved area of pronotum blackish fuscous; rostrum with apical segment fuscous; forewings (Figs. 1-4, 17) opaque, veins brown, a short costal band near base brown (the band sometimes missing), apex and areas surrounding the cross veins at basal 1/3 and apical 1/3 suffused with brown or fuscous, setae on veins brown; hindwings (Fig. 18) hyaline, veins and setae on veins brown; abdomen with lateral margins and lateral sides of hind margins of tergites and lateral margins of sternites blackish fuscous, tergites somewhat brownish; pygofer with dorsal, hind and ventral margins blackish fuscous, male parameres with



Figs. 15-25. *Paricanoides orientalis* Liang sp. nov. 15. head, pronotum and mesonotum, dorsal view; 16. head, ventral view; 17. right forewing; 18. right hindwing; 19-25. male genitalia. 19. pygofer, lateral view; 20. pygofer, ventral view; 21. anal tube, dorsal view; 22. left paramere, lateral view; 23. aedeagal shaft, left lateral view; 24. aedeagal shaft, right lateral view; 25. aedeagal shaft, dorsal view. Abbreviations: AMP = apical membranous process of penis; APPen = apical process of penis; APPer = apical process of periandrium; BPPer = branched process of periandrium; MPPer = middle process of periandrium; Pen = penis; Per = periandrium. Scale bars = 0.5 mm.

apical 1/4 blackish fuscous; apices and bases of fore and middle tibiae fuscous, spines on hind legs black-tipped, claws black.

External characters as in generic description above. Metatarsal segment II with 6 spines apically. There are some variations in the number of the apical cells in forewings. In one male paratype specimen collected from Tonkin, Vietnam, the right forewing has 9 apical cells but the left forewing has 10 (resulting from M1 also branched). In one female specimen (Fig. 4) taken at Blao, Vietnam, both the left and right forewings have the R unbranched apically and have only 8 apical cells.

Male genitalia with pygofer narrow and high, wider dorsally than ventrally, with dorsal posterior margin angularly produced posteriorly in lateral view; dorsal margin deeply excavated to accommodate anal tube in dorsal view (Fig. 19); ventral margin strongly excavated anteriorly to accommodate parameres in ventral view (Fig. 20). Anal tube elongate, narrow and slender in dorsal view, apex somewhat claw-like in dorsolateral

view (Figs. 19, 21); anal style relatively short and small, not reaching beyond the apical ventral margin of anal tube. Parameres (Figs. 19, 20, 22) symmetrical, relatively large, short and broad, apex expanded and relatively broad, somewhat angulately produced caudad in lateral view, with a stout, inward directed process on upper margin at apex, beyond this stout process with a small, lateroventrally directed, spinous process; upper margin with a very small nodal process near base and an acute, dorsally directed process at middle in lateral view. Aedeagus (Figs. 19, 23-25) somewhat elongate, robust and mostly sclerotized, asymmetrical, periandrium surrounding penis at base, distally attached to penis ventrally, with two dorsally directed processes at apex and one posterodorsally directed process near middle at left side; penis with one membranous process and one dorsally directed process at apex (Figs. 23-25) and a branched process at right side at apex: one branch relatively short, directed dorsally, the other branch very elongate, tapered from base to

apex, strongly directed anteriorly, with apical part curved posterodorsally (Fig. 24).

Female genitalia with anal tube narrow and short, shorter than third valvulae; anal style very short and small, not extending beyond apical ventral margin of anal tube; third valvulae each having 15 visible, short teeth apically and one small outer tooth apically.

Etymology. This new species is named for its distribution in the Oriental region.

Distribution. South China (Hainan Island) and Vietnam (Tonkin, Blao).

Specimens examined. Holotype ♂, CHINA: Hainan Island, Jianfengling (18°7'N, 108°8'E), Tianchi, 750 m, 24.iii.1980 (S. Y. Wang) (IZCAS). Paratypes. CHINA: Hainan Island, 1♀, same data as holotype except 900 m, 11.iv.1980 (IZCAS); 1♂, Jianfengling, 12.iv.1980 (S. Z. Ren) (NU). [VIETNAM]: 2♂♂, Tonkin, Mont Bavi, 900-1000 m, viii.1940 (P. A. de Cooman) (IZCAS).

Other specimens examined. VIETNAM: 1♀, Blao (Balao), 500 m, 14-21.x.1960 (C. M. Yoshimoto) (BPBM). This female specimen is externally very similar to the above type specimens. But both the left and right forewings of this female specimen have vein R unbranched apically and have only 8 apical cells (Fig. 4). In addition, the metatarsal segment II is somewhat covered ventrally with tomenta and has 8 black-tipped spines apically.

Remarks. This species can be distinguished from other known tropiduchids from China and adjacent regions by its short and broad vertex (Figs. 1-4, 15), vertex and frons without median carina (Figs. 15, 16), frons with an inverse U-shaped, reddish stripe (Fig. 16), distinct forewing venation (Figs. 1-4, 17) and the shape of the male genitalia (Figs. 19-25). It can be separated from the other species in the genus, *P. dalatensis* from Vietnam (Dalat) (see below) by the vertex relatively broader and shorter (Fig. 15); metatarsal segment II with 6 apical spines; and the shape of the male genitalia, especially anal tube relatively shorter and narrower in dorsal view (Fig. 21), parameres with upper margin with a stout, inward directed process at apex (Figs. 19, 22), and different processes on aedeagus as noted above (Figs. 19, 23-25).

Paricanoides dalatensis Liang sp. nov.
(Figs. 5-14, 26-33)

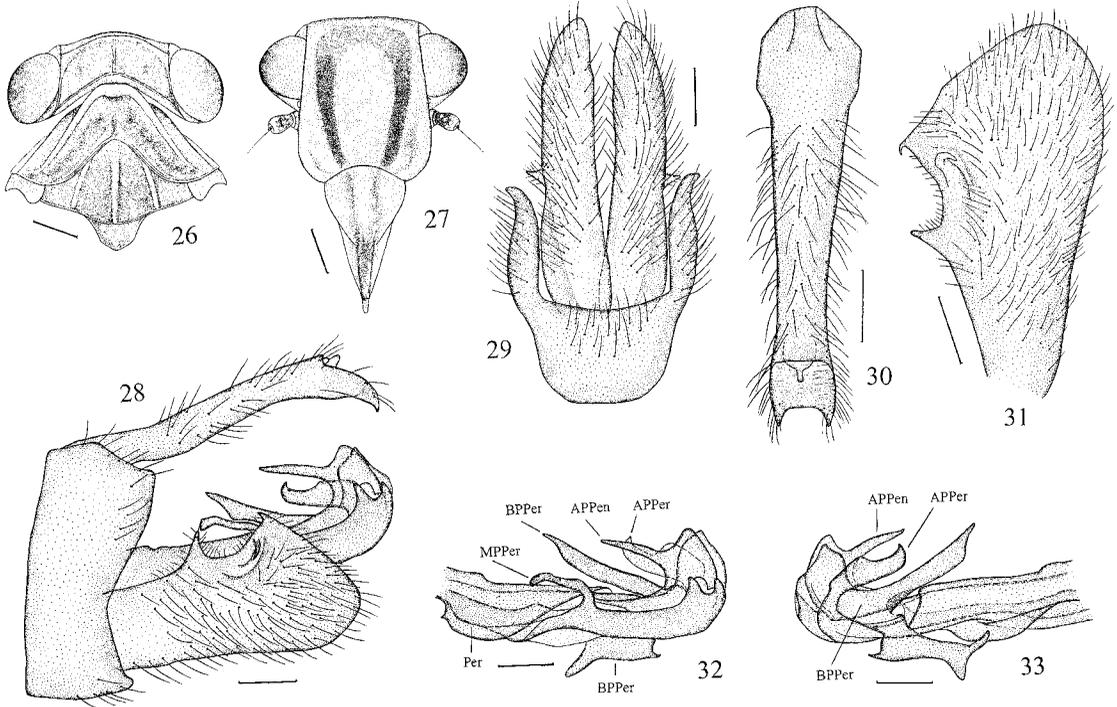
Description. Length (from apex of vertex to tip of forewings): ♂ 13.50 mm, ♀ 14.00 mm. General color and external appearance similar to the above new species, with vertex having very fine median carina, pronotum with very faint median carina, apex of frons and carinae on pronotum and mesonotum distinctly reddish, inverse U-shaped stripe on frons with lateral branches dark brown or fuscous; forewings without basal brown band at basal costal area; tarsal segments of fore

and middle legs dark brown; vertex relatively narrow; metatarsal segment II with 7 black-tipped spines apically.

Male genitalia with pygofer (Fig. 28) in lateral view narrow and high, wider dorsally than ventrally, with dorsal posterior margin angularly produced posteriorly, dorsal margin deeply excavated anteriorly to accommodate anal tube in dorsal view, ventral margin very strongly excavated anteriorly to accommodate parameres in ventral view (Fig. 29). Anal tube (Figs. 28, 30) elongate, with base relatively broad, gradually narrowing toward apex with apex slightly expanded, apex nearly claw-like in dorsolateral view; anal style (Figs. 28, 30) very small and short, not reaching beyond apical ventral margin of anal tube. Parameres (Figs. 28, 29, 31) relatively short and broad (Figs. 28, 31), apex very broadly produced posteriorly, upper margin with a very small, anterodorsally directed, acute process at apex, beyond this acute process with a small, lateroventrally directed, spinous process, with a posterodorsally directed, triangular process on upper margin near middle in lateral view (Fig. 28); ventral margin relatively straight in lateral view. Aedeagus (Figs. 28, 32, 33) asymmetrical, perianthrium enclosing penis at basal 1/2 and surrounding penis ventrally at apical 1/2, apex excavated medially at left side (Figs. 28, 32), with one anterodorsally directed process near middle at left side (Figs. 28, 32) and one apical, anterodorsally directed process at right side (Fig. 33); penis with one apical, anterodorsally directed process with very broad laminate base at left side (Figs. 28, 32) and one subapical branched process at right side; one process relatively elongate and anterodorsally directed, the other process directed anteroventrally with somewhat forked apex (Fig. 33).

Female genitalia (Fig. 14) with third valvulae each having 16-17 short stout teeth apically and one small outer tooth apically.

Eggs. Overall appearance elongate-oval (Fig. 5), length 1.32-1.45 mm; width near bottom 0.48-0.65 mm. The egg surface has two main regions: a specialized area and an unspecialized egg capsule (Figs. 5, 7). The specialized area is characterized by a large respiratory plate containing the operculum and a micropylar horn in apical portion (Figs. 5-7). The operculum (Figs. 5, 7) is ellipsoidal in shape, about 0.48-0.56 mm wide (including the marginal collar). The operculum has a clear marginal collar with the marginal length of the collar being about 88-100 μ (Figs. 5, 7) but has a clear boundary separating the operculum from the surrounding egg surface and facilitating larval eclosion (Fig. 9). The surface of the operculum is covered with many respiratory pores (Figs. 7, 9-11). They are mostly oval or rounded with a few being ellipsoidal. The opening of the rounded or oval pores measures about 2.2-5.6 μ wide and the opening of the elongate pores measures about 6.0-



Figs. 26-33. *Paricanoides dalatensis* Liang sp. nov. 26. head, pronotum and mesonotum, dorsal view; 27. head, ventral view; 28. pygofer, lateral view; 29. pygofer, ventral view; 30. anal tube, dorsal view; 31. left paramere, lateral view; 32. aedeagal shaft, left lateral view; 33. aedeagal shaft, right lateral view. Abbreviations: APPen = apical process of penis; APPer = apical process of periandrium; BPPer = branched process of periandrium; MPPer = middle process of periandrium; Per = periandrium. Scale bars = 0.5 mm.

12.8 μ long. The apical micropylar horn (Figs. 5, 6) is relatively long (about 0.28-0.36 mm in length) and narrows gradually towards its apex with the extreme apex distinctly expanded and hollow internally. The opening of the apical micropylar horn is about 27.0-28.8 μ . The chorion surface is covered with a reticulate, polygonal pattern (Figs. 12, 13).

Information on the eggs of Tropicuchidae is very limited. The egg of *Paricanoides dalatensis* is generally similar to that of *Ommatissus binotatus* Fieber (Guglielmino et al. 1997) and *Tambinia rubrolineata* Liang (Liang & Jiang 2003) but differs in the operculum having a distinct collar and different shapes of the openings of the respiratory pores on the operculum and the respiratory horn being very long (Figs. 5-7, 9-13).

Etymology. This new species is named for its occurrence in Dalat, Vietnam.

Distribution. Vietnam (Dalat).

Specimens examined. Holotype δ , VIETNAM: Dalat, 6 km S., 1400-1500 m, 9.vi-7.vii.1961 (N. R. Spencer) (BPBM). Paratype. VIETNAM: 1 \varnothing , same data as holotype (BPBM).

Remarks. This species can be distinguished from the above new species by the vertex rela-

tively narrower and longer (Fig. 26); metatarsal segment II with 8 apical spines; and the shape of the male genitalia, especially the anal tube relatively longer and broader in dorsal view (Fig. 30), parameres with an acute process on upper margin at apex (Fig. 31) and the distinct processes on aedeagus as noted above (Figs. 28-33).

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**ECOLOGY AND CONTROL OF *NEOSORIUS BREVIPENNIS*
(COLEOPTERA: STAPHYLINIDAE) ON TURF GRASS IN SOUTH AFRICA**

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Very little information on the ecology and pest status of the fossorial rove beetle, *Neosorius brevipennis* Fagel is available (Smetana 1985). These beetles tunnel underground and lay their eggs in clusters of three to ten in the blind ends of tunnels. It was found by sampling and observation that *N. brevipennis* were responsible for casting mounds on golf course putting greens in Johannesburg and Pretoria (Schoeman 1997). Soil castings may damage mowing equipment, interfere with play by deflecting putts, and are objectionable for aesthetic reasons. A study of a fossorial rove beetle (*Orosius planifrons* Leconte), responsible for casting mounds on greens at the Tucson Country Club, Tuscon, AZ, USA, was conducted in the late 1970s. That study included ecological and behavioral analysis and concluded that *O. planifrons* requires high soil moisture and probably feeds on soil microbes (Smith et al. 1978). The authors discussed cultural control but no chemical or biological control methods were addressed.

The objectives of this study were to determine the annual population densities and soil profile distributions of *N. brevipennis* on bent grass (*Agrostis stolonifera* L.) and kikuyu grass (*Penisetum clandestinum* Hochst. ex. Chiov.). The efficacy of chemical controls for *N. brevipennis* was also investigated.

Neosorius brevipennis was sampled at the Wingate Park Country Club (WPCC) in Pretoria, Gauteng, South Africa (25°44'S, 28°15'E). Chemical trials were conducted at Kensington golf course in Johannesburg, Gauteng, South Africa (28°40'S, 25°10'E). The study was conducted from November 1999 to October 2000.

Five random samples were taken with a putting green hole cutter (diameter: 110 mm and

depth: 100 mm) on a green (bent grass) and on a fairway (kikuyu grass), respectively, to examine the distribution and population densities of adult and immature rove beetles in the soil profile. Eggs were not included in the study. Soil cores were examined in 25 mm thick sections and all stages found at each depth were recorded. The 10 samples were collected and analyzed monthly from November 1999 to October 2000 to determine the population density of *N. brevipennis* throughout the year. The distribution of *N. brevipennis* between the upper 50 mm and 51-100 mm of the soil profile and between green (bent grass) and fairway (kikuyu grass) samples were compared using the non-parametric Kruskal-Wallis test.

Ten random plots of 0.25 m² (0.5 m × 0.5 m) were sampled to determine the mean number of casting mounds per 0.25 m². After assessments were made, 100 individual mounds were collected in poly-top-containers and the average dry mass per mound was measured in the laboratory with a Sartorius scale. Data were collected mid-day on putting green 9 at WPCC in mid April 2000, at an average surface temperature of 25.9°C.

The chemical trials were conducted at the beginning of 2000 (8 January-3 March). The infested putting green 12 on Kensington golf course was divided into six blocks of 28 m² (3.00 m × 9.33 m). Five chemicals (carbaryl, fipronil, imidacloprid, isofenphos and azinphos-methyl), formulated as a WP, SC, SC, EC and EC, respectively, were tested. Blocks were randomly allocated to each chemical and a control (untreated) area. Insecticides were applied to the turf surface with a backpack sprayer at the typical turf rate (Table 1). Application was followed by irrigation (using the golf course irrigation system) for 9 min (equivalent of

TABLE 1. THE MEAN NUMBER OF SOIL PUSH-UPS PRESENT (AT MID-DAY) PER 0.11 m². MEANS WITH LETTERS IN COMMON, ARE NOT SIGNIFICANTLY DIFFERENT (P > 0.05).

Chemical (G AI/ha)	Mean number of mounds per week							
	05 DAT	12 DAT	19 DAT	26 DAT	33 DAT	41 DAT	47 DAT	54 DAT
Carbaryl (600)	0.8 a	0.8 a	0.8 a	3.0 ab	3.4 ab	5.6 ab	4.6 a	3.8 ab
Fipronil (75)	10.2 b	24.8 c	7.2 ab	17.4 bc	21.2 c	18.0 c	21.0 d	20.4 c
Imidacloprid (350)	5.4 ab	5.4 ab	2.4 ab	2.4 ab	1.6 a	2.4 ab	2.4 a	1.4 a
Isofenphos (2000)	0 a	0 a	0 a	0 a	0 a	0 a	0 a	0 a
Azinphosmethyl (2100)	19.4 c	18.0 bc	9.0 b	8.4 ab	15.2 bc	15.4 b	10.8 b	9.8 b
Control	40.2 d	53.2 e	39.4 d	39.0 d	34.2 d	53.4 e	49.6 f	45.0 d

10 mm precipitation) to water the insecticides into the soil. The control block was also watered with the same volume. The treated and untreated blocks were monitored weekly (at mid-day) for soil mounds or "push-ups" for eight consecutive weeks, starting 5 d after the single chemical application. Five randomly selected 0.11 m² (a circle with a diameter of 375 mm) areas in each block were used to count the number of soil mounds present each week (to test the temporal efficiency of the different chemicals). A MANOVA (Multivariate Analysis of Variance) and post hoc Tukey HSD (Honest Significant Difference) test was used to separate means. The statistical analysis of all the data was conducted on the software program "Statistica", Version: 5 (1995) (Statsoft, Inc.).

RESULTS

Significantly more *N. brevipennis* adults and larvae were found in the soil from the soil surface to a depth of 50 mm (81.05% of beetles sampled) than at a depth of 51 to 100 mm (18.95% of beetles sampled) in the soil profile (Kruskal-Wallis, $p = 0.0011$). The annual population density variation of *N. brevipennis* is shown in Fig. 1. The relative occurrence of the adults and larvae, over an annual period, indicates the beetles over winter as adults (Fig. 1). Converting numbers to square meters, the maximum (\pm S.E.) number of rove beetles per square meter was 1620.49 ± 562.35 in October (early summer) and the minimum (\pm S.E.) number was 294.63 ± 46.53 , in June (winter). There was no significant difference between the green (bent grass) and fairway (kikuyu grass) infestation densities (Kruskal-Wallis, $p = 0.10$) (data not shown).

The average number of mounds (\pm S.E.) was 61.30 ± 4.78 per 0.25 m² (or 245.20 ± 19.12 m²) with a mean mound mass (\pm S.E.) of 40 ± 1.64 mg.

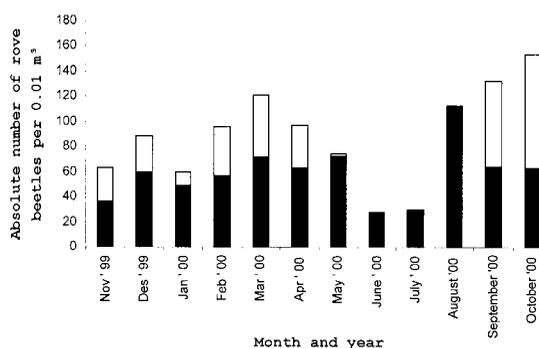


Fig. 1. The proportion of adults (black) and larvae (white) representing the absolute monthly numbers of *N. brevipennis* per 0.01 m² (10 samples with a diameter of 110 mm and 100 mm deep) over an annual period (November 1999 to October 2000).

The average number of mounds (\pm S.E.) equals when standardized to number per square meter.

Table 1 summarizes the weekly mean number of mounds in different insecticide treatments, as well as significant differences between them (MANOVA; Tukey HSD). All the insecticide treated blocks had significantly less soil mounds than the untreated control block over the monitoring period. The isofenphos treated block had no soil mounds present in the eight weeks of monitoring. The soil mounds on the carbaryl and imidacloprid treated blocks were not significantly higher than the isofenphos treated block over the sampling period. The azinphos-methyl and the fipronil treatments were generally significantly less effective than any of the other treatments, but had significantly fewer mounds than the untreated.

DISCUSSION

Populations of adult and larval *N. brevipennis* were concentrated just beneath the grass surface up to a depth of 50 mm in the soil profile. The highest density of rove beetles occurred in the warm, moist, spring and early summer months (Aug.-Oct.). The data suggested that these beetles overwintered as adults. The life expectancy and life cycle length is unknown. The beetles were found in similar numbers on bent and kikuyu grass, with initial infestation usually concentrated on green surrounds (kikuyu grass).

As a result of the tunnelling activity of *N. brevipennis*, aesthetically unacceptable soil mounds are pushed up on the grass surface. The average number of mounds on a putting green per square meter was 245, but up to 400 casts per meter has been reported (Schoeman 1997).

All of the chemicals tested were effective at reducing mounds relative to the untreated control area. Isofenphos was the most effective, resulting in no symptoms (mounds) of infestation for at least 8 wk after application. Carbaryl and imidacloprid were second most and equally effective. Relative to isofenphos, however, carbaryl was more effective than imidacloprid. Azinphos-methyl, followed by fipronil, were the least effective chemicals in the test group.

SUMMARY

The fossorial rove beetle, *N. brevipennis*, tunnels underground primarily in the top 50 mm of the soil profile of bent and kikuyu grass and causes soil mounds on the surface. It is most abundant in late spring and early summer. The most effective insecticide for controlling *N. brevipennis* is isofenphos, but carbaryl and imidacloprid also proved effective. Azinphos-methyl and fipronil and were not found to be highly effective.

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INVASION OF *PARATACHARDINA LOBATA LOBATA* (HEMIPTERA: KERRIIDAE) IN SOUTH FLORIDA: A SNAPSHOT SAMPLE OF AN INFESTATION IN A RESIDENTIAL YARD

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The lobate lac scale, native to Sri Lanka and India (Varshney 1976), was first detected in Davie, Broward County Florida in August 1999 and then in Miami Dade during March 2000 (Hammon 2001). By the spring of 2002, the insect began to appear in alarming densities on many different host plants in Broward County. To obtain an idea of the current and potential infestation of this scale on plants in South Florida, a "snap-shot" sample was made in a single Ft. Lauderdale residential yard known to be infested with the scale during July, 2002. Although modest in terms of area examined and duration of study, this sample offers a compelling picture of the scale's extreme polyphagy and may provide indications of relative susceptibility of different plants and plant groups.

The 1/3 acre yard examined was selected because of its diverse plantings of tropical fruit, native plants, and horticultural plants including important landscape trees and shrubs. It was also chosen because of the absence of pesticide use which might influence infestation, although county mosquito control fogging trucks operate periodically within 30 meters of the property, particularly during the summer. A total of 67 woody plant species in 30 plant families were examined for presence of the scale. A total of 83 individual plants were examined and seven species were sampled more than once. Plants sampled were at least one meter tall and present in the yard for at least one year. Each plant was scanned for about 30 seconds, except for orange and tangelo, which were examined for about five minutes because of their economic importance. If the scale was found, estimates of infestation were made by judging the number of morphologically distinct mature females in 30 cm length of branch as follows. Heavy infestations had more than 100 scales per 30 cm, moderate infestations had between 10 and 100, and light infestations had fewer than 10.

The scale was found in 37/67 (55%) of the plant species in 19/30 (63.3%) of the plant families (Table 1). Of the attacked species, 16% (6/37) had plants rated as heavily infested, 40% (15/37) had moderately infested plants, and 62% (23/37) had lightly infested plants. Of the 83 individual plants examined, 46 or 55% were infested. The most severely impacted plant was the native wax myrtle (*Myrica cerifera* L.); three of the five plants examined had been killed and the other two were dying. The scale completely covered branches of these plants. Other heavily infested species in-

cluded native wild coffee (*Psychotria nervosa* Sw.), ornamental *Michelia* sp. and common hibiscus, and the fruit tree carambola (*Averrhoa carambola* L.). All of these exhibited branch dieback. Large landscape trees, such as native laurel oak and exotic black olive, bore moderate infestations. All four mango varieties (Carrie, Jakarta, Dot and Valencia Pride) were infested and three had moderate infestations. Grapefruit and kumquat had light levels of the scale, while sweet orange and tangelo were free of the insect. Emperor lychee was attacked but Brewster lychee was not. The three annonaceous fruits, sugar apple, sour sop and atemoya were all attacked. One species, wild coffee, experienced the full range of infestation levels from absence to heavy. Attacked species belong to a diverse spectrum of unrelated families from the primitive Magnoliaceae and Lauraceae to the advanced Rubiaceae. Of the 17 families with more than one species in the sample, four had all species attacked, four had none attacked, and nine had both attacked and unattacked species. Seven of eight Myrtaceae and three of four Rubiaceae were infested by the scale. Three of the seven Rutaceae present were infested. Three of seven genera with multiple species had both attacked and unattacked species, while plants in the other four genera were either all attacked or unattacked.

Because it is unknown how long the scale has been at this site, infestation and level of infestation on particular plant species may reflect the state of invasion and degree of population growth. Uninfested and lightly infested plants may reflect preference of the scale for other plants, rather than absence of susceptibility. For this reason, presence of the scale in the sample is more important than its absence. What is clear is that the scale attacked the majority of species and families represented in the yard as well as the majority of individual plants examined. It also used a wide variety of plant types including native species, commercial fruit, and important landscape trees and shrubs. *Paratacharina lobata lobata* is becoming a serious pest, due to rapid rate of spread, wide host range, and severe impacts to plants such as branch dieback and death of some hosts.

Research is urgently needed to determine how to control the lobate lac scale and how, if possible, to limit its spread. Control research should include both chemical and biological control. Infestation of native plants indicates the scale's ability to invade natural areas where chemical control

TABLE 1. PLANTS EXAMINED FOR LOBATE LAC SCALE INFESTATION IN A FT. LAUDERDALE RESIDENTIAL YARD DURING JULY 2002.

Family Species	Common name	Type of plant	Infested	Number infested			
				High	Medium	Light	None
Aceraceae							
<i>Acer rubrum</i> L.	Red maple	Native-ornamental tree	No				1
Apocynaceae							
<i>Trachelopermum jasminoides</i> (Lindl) Lem.	Confederate jasmine	Ornamental vine	No				1
Anacardiaceae							
<i>Mangifera indica</i> L.	Mango	Fruit tree	Yes		3	1	
<i>Schinus terebinthifolius</i> Raddi	Brazilian pepper	Ornamental tree	Yes			1	
<i>Toxicodendron radicans</i> (L.) Kuntze	Poison ivy	Native vine and weed	No				1
Annonaceae							
<i>Annona squamosa</i> L.	Sugar apple	Fruit tree	Yes		1		
<i>Annona muricata</i> L.	Soursop	Fruit tree	Yes		1		
<i>Annona</i> × <i>Atemoya</i>	Atemoya	Fruit tree	Yes			1	
Clusiaceae							
<i>Rheedia aristata</i> Griseb.	Rheedia	Fruit tree	Yes			1	
<i>Rheedia</i> sp.	Rheedia	Fruit shrub	Yes		1	2	
Combretaceae							
<i>Bucida buceras</i> L.	Black olive	Landscape tree	Yes		1		
<i>Terminalia catappa</i> L.	Tropical almond	Ornamental tree	Yes			2	
Euphorbiaceae							
<i>Bischofia javanica</i> Blume	Bischofia	Landscape tree	No				2
<i>Codiaeum variegatum</i> (L.) Blume	Croton	Ornamental shrub	No				3
<i>Sauropus androgynus</i> (L.) Merr.	Sauropus	Edible leaved shrub	No				1
Fabaceae							
<i>Acacia farnesiana</i> (L.) Willd.	Sweet acacia	Native-ornamental shrub	No				1
<i>Cassia pendula</i> Willd.	Christmas senna	Ornamental shrub	No				1
Fagaceae							
<i>Quercus laurifolia</i> Michx.	Laurel oak	Native-landscape tree	Yes		2	1	
Lamiaceae							
<i>Ocimum</i> sp.	Thai basil	Spice shrub	Yes			1	
<i>Rosmarinus officinalis</i> L.	Rosemary	Spice shrub	No				2
Lauraceae							
<i>Cinnamomum zeylanicum</i> Blume	Cinnamon	Ornamental shrub	Yes			1	
<i>Laurus nobilis</i> L.	Bay leaf	Spice shrub	Yes			1	
Magnoliaceae							
<i>Michelia</i> sp.	Michelia	Ornamental shrub	Yes	1			

TABLE 1. (CONTINUED) PLANTS EXAMINED FOR LOBATE LAC SCALE INFESTATION IN A FT. LAUDERDALE RESIDENTIAL YARD DURING JULY 2002.

Family Species	Common name	Type of plant	Infested	Number infested			
				High	Medium	Light	None
Malvaceae							
<i>Hibiscus rosa-sinensis</i> L.	Hibiscus	Ornamental shrub	Yes	1			
Meliaceae							
<i>Agalia odorata</i> Lour.	Mi lan	Ornamental shrub	No				1
Moraceae							
<i>Artocarpus heterophyllus</i> Lam.	Jakfruit	Fruit tree	No				
<i>Ficus benjamina</i> L.	Benjamin fig	Landscape fig	Yes			1	
<i>Morus</i> X.	Mulberry	Fruit tree	No				2
Myricaceae							
<i>Myrica cerifera</i> L.	Wax myrtle	Native-ornamental shrub	Yes	1			
Myrtaceae							
<i>Calyptranthes pallens</i> Griseb.	Spicewood	Native-ornamental shrub	Yes		1		
<i>Eugenia brasiliensis</i> Lam.	Grumichama	Fruit tree	Yes		1		
<i>Eugenia uniflora</i> L.	Surinam cherry	Landscape hedge plant	Yes			2	
<i>Eugenia aggregata</i> (Vell.) Kiaersk.	Cherry-Rio Grande	Fruit shrub	No				1
<i>Myrciaria cauliflora</i> (C. Martius)	Jaboticaba	Fruit tree	Yes			1	
<i>Myrciaria</i> sp.	Yellow jaboticaba	Fruit shrub	Yes			1	
<i>Pimenta dioica</i> (L.) Merr.	All spice	Spice shrub	Yes			1	
<i>Pimenta racemosa</i> (Miller) J. Moore	Bay rum	Spice shrub	Yes			1	
Nyctaginaceae							
<i>Bougainvillea</i> X.	Bougainvillea	Ornamental vine	No				2
Oleaceae							
<i>Jasminum gracillimum</i> Hook. F.	Pinwheel jasmine	Ornamental shrub	No				1
<i>Osmanthus fragans</i> Lour.	Sweet olive	Ornamental shrub	No				1
Oxalidaceae							
<i>Averrhoa carambola</i> L.	Carambola	Fruti tree	Yes	1	1		
Poaceaeae							
<i>Bambusa vulgaris</i> J.C. Wendl.	Golden bamboo	Ornamental	No				1
<i>Phyllostachys nigra</i> (Lodd. & Lindl.) Munro	Black bamboo	Ornamental	No				1
Polygonaceae							
<i>Coccoloba unifera</i> (L.) L.	Sea grape	Native-ornamental tree	No				1
Rosaceae							
<i>Eriobotrya japonica</i> (Thunb.) Lindl.	Loquat	Fruit tree	No				1
Rubiceae							
<i>Gardenia jasminoides</i> Ellis	Gardenia	Ornamental shrub	Yes		1		

TABLE 1. (CONTINUED) PLANTS EXAMINED FOR LOBATE LAC SCALE INFESTATION IN A FT. LAUDERDALE RESIDENTIAL YARD DURING JULY 2002.

Family Species	Common name	Type of plant	Infested	Number infested			
				High	Medium	Light	None
<i>Hamelia patens</i> Jacq.	Firebush	Native-ornamental shrub	Yes		1		
<i>Ixora coccinea</i> L.	Ixora	Ornamental shrub	No				3
<i>Psychotria nervosa</i> Sw.	Wild coffee	Native-ornamental shrub	Yes	2	5	2	2
Rutaceae							
<i>Citrus</i> X.	Grapefruit	Fruit tree	Yes			1	
<i>Citrus</i> X. <i>tangelo</i>	Tangelo	Fruit tree	No				1
<i>Citrus sinensis</i> (L.) Osbeck	Sweet orange	Fruit tree	No				1
<i>Clausena lansium</i> (Lour.) Skeels	Wampi	Fruit tree	Yes			1	
<i>Fortunella japonicum</i> (Thunb.) Swingle	Kumquat	Fruit tree	Yes			1	
<i>Murraya paniculata</i> (L.) Jack	Orange jasmine	Ornamental shrub	No				1
<i>Zanthoxylum fagara</i> (L.) Sarg.	Wild lime	Native shrub	No				1
Sapindaceae							
<i>Dimocarpus longan</i> Lour.	Longan	Fruit tree	No				1
<i>Litchi sinensis</i> Sonn.	Lychee	Fruit tree	Yes		1		1
Sapotaceae							
<i>Manilkara zapota</i> (L.) Van Royen	Sapodilla	Fruit tree	No				1
<i>Synsepalum dulcificum</i> (Schumach. & Thonn.) Daniell	Miracle fruit	Fruit shrub	Yes	1	1		
Solanaceae							
<i>Brunfelsia</i> sp.	None	Ornamental shrub	Yes			1	
<i>Brunfelsia lactea</i> Krug. Urb.	None	Ornamental shrub	No				1
<i>Brunfelsia nitida</i> Benth.	Lady of the night	Ornamental shrub	Yes		1		
<i>Cestrum nocturnum</i> L.	Night blooming jasmine	Ornamental shrub	Yes			1	
Verbenaceae							
<i>Citharexylum spinosum</i> L.	Fiddlewood	Native-ornamental shrub	No				1
Vitaceae							
<i>Parthenocissus quinquefolia</i> (L.) Planch.	Virginia creeper	Native vine	Yes			1	

may be difficult, cost prohibitive or inappropriate because of potential harm to non-target organisms. Indeed, preliminary examination of several preserves, such as Secret Woods Nature Center in Broward County, indicates a serious level of infestation of native species (Howard, unpublished data; Pemberton, unpublished data). During October and November 2002, the lobate lac scale was discovered in Everglades National Park, Big Cypress National Wildlife Refuge and Loxahatchee National Wildlife Refuge (Pemberton, unpublished data). For additional information on this important pest, including known host plants as of October 2002, see the recently posted Featured Creatures website (Howard et al. 2002). Biological control may offer a long term solution (Pemberton 2003).

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SUMMARY

A recent insect invader in South Florida, the lobate lac scale (*Paratachardina lobata lobata*) attacked 55% (37/67) of the plant species in 63%

(19/30) families at a sampled site. Many important plants in southern Florida were attacked including: tropical fruits (grapefruit, mango, lychee and sugar apple), native plants (wild coffee, laurel oak and wax myrtle), and important landscape trees and shrubs (black olive, hibiscus, Surinam cherry, and gardenia). Some plants such as wax myrtle are killed by the scale. Research to develop control methods is urgently needed.

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A SIMPLE CHARACTER FOR SEX DIFFERENTIATION OF PUPAE AND PUPAL EXUVIAE OF THE DOGWOOD BORER (LEPIDOPTERA: SESIIDAE)

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The dogwood borer, *Synanthedon scitula* (Harris) (Lepidoptera: Sesiidae), has the broadest host range of all species of Sesiidae and is an economically important pest of numerous ornamental, fruit and nut trees (Engelhardt 1932; Eichlin & Duckworth 1988; Johnson & Lyon 1991). Dogwood borer has become an important indirect pest of apple in the eastern United States and Canada (Riedl et al. 1985; Warner & Hay 1985; Weires 1986; Pfeiffer & Killian 1999; Kain & Straub 2001) due to increased plantings on clonal, size-controlling rootstocks in high-density apple orchards (Riedl et al. 1985; Kain & Straub 2001). These rootstocks promote formation of adventitious root primordia or burr knots near the graft union at the base of the tree (Rom 1970, 1973) that appear to be preferred oviposition sites for female dogwood borer (Riedl et al. 1985; Warner & Hay 1985; Kain & Straub 2001). Continuous infestations lead to larval feeding over consecutive seasons resulting in consumption of burr knot tissue and feeding in the cambial layer, ultimately leading to tree death from girdling (Weires 1986). The increasingly important pest status of dogwood borer has led to recent research efforts into management options (Kain & Straub 2001) as well as refinement of the pheromone-based monitoring system (Bergh & Leskey 2003). Adult male and female dogwood borers can be differentiated by the

more robust abdomen with mostly yellow coloration on ventral segments four, five and six, and the more yellow brush-like anal tuft of females (Eichlin & Duckworth 1988). Sex differentiation of the pupal stage of dogwood borer has never been described specifically, but a generalized description of pupae of sesiid species by Eichlin & Duckworth (1988) indicates that pupae are highly modified to facilitate extrication from host plant tissue, with double rows of posteriorly projecting spines on abdominal segments 2-6 and on segment 7 of males, and single rows on remaining segments 8-10.

Pupae and pupal exuviae of dogwood borer were obtained by excavating larvae from burr knot tissue of apple trees with obvious signs of infestation including frass and entry wounds in Jefferson and Berkeley Counties, WV, USA. Larvae were reared individually in the laboratory on general purpose Lepidopteran diet (Bioserv, Frenchtown, NJ) in an environmental chamber at 25°C and 14L:10D. We followed 20 pupae to adulthood and determined the sex of moths, as described by Eichlin & Duckworth (1988). The pupal exuviae left by each moth was then examined under Leica GZ4 (7-30×) and Nikon SMZ 1500 (7.5-112.5×) stereomicroscopes for sex-related differences in pupal characteristics. These differences were then confirmed on live pupae. Microscopic examination revealed distinct differences between sexes in the

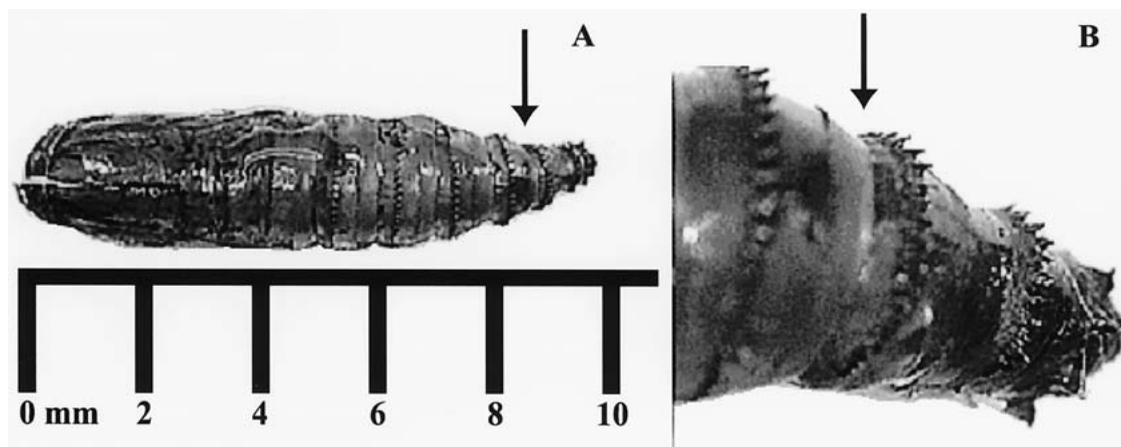


Fig. 1. (A) Caudal view of entire pupal exuviae (10×) and (B) lateral view (50×) of fused terminal abdominal segment (segments 8-10) with 3 rows of posteriorly projecting spines of the pupal exuviae of the male dogwood borer. Arrows indicates suture between fused segments.

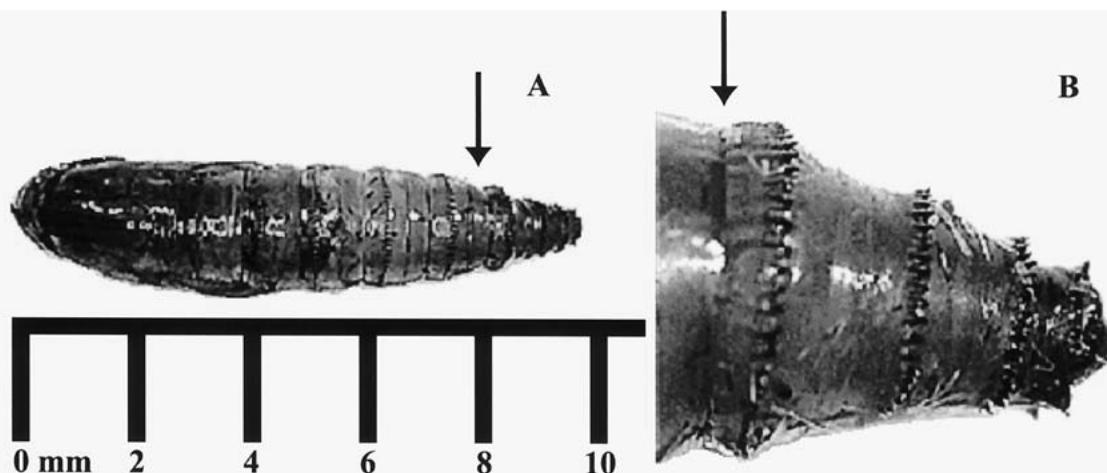


Fig. 2. (A) Caudal view of entire pupal exuviae (10 \times) and (B) lateral view (50 \times) of fused terminal abdominal segment (segments 7-10) with 4 rows of posteriorly projecting spines of the pupal exuviae of the female dogwood borer. Arrows indicates suture between fused segments.

fused terminal abdominal segment. In males, this fused segment is composed of segments 8-10 and has three distinct single rows of posteriorly projecting spines (Fig. 1). By contrast, in females, it is composed of segments 7-10 and has four distinct single rows of posteriorly projecting spines (Fig. 2). These differences allow easy and accurate sex differentiation of dogwood borer pupal exuviae and pupae. The total number of rows of spines on the abdomen of both males and females was in agreement with the generalized description of pupae of sesiid species (Eichlin & Duckworth 1988). Female and male pupae had 14 and 15 rows, respectively. However, Eichlin & Duckworth (1988) made no mention of variation among species with regard to the presence of fused abdominal segments and/or the number of rows of spines present on the fused abdominal segments. Counts of the total number of rows of spines on the abdomen of pupae as described by Eichlin & Duckworth (1988) could be used to differentiate pupal sex. However, this method is more cumbersome and potentially less reliable because of the greater number of rows to be counted and because the second row of spines on abdominal segments 2 and 3 is fairly subtle on the dogwood borer, contributing to misidentifications.

Our method of sexing pupae was very useful for determining the gender of adults to be used in laboratory experiments studying mating behavior of the dogwood borer. Furthermore, this character was useful in identifying the sex of pupal exuviae recovered from apple trees in commercial orchards to establish seasonal phenology and to examine protandry. Sexual dimorphism of the fused terminal abdominal segments of pupae of other sesiid species may exist, although it was not examined in this study.

We thank Starker E. Wright for preparing photographs, and Jean Englemann and Torri Thomas for excellent technical assistance. We thank Dr. Henry Hogmire and Dave Kain for reviewing an earlier version of this manuscript.

SUMMARY

The sex of dogwood borer pupae and pupal exuviae can be easily differentiated based on characteristics of the fused terminal abdominal segment. In males, it is composed of segments 8-10 and has three distinct rows of posteriorly projecting spines. By contrast, in females, the fused terminal abdominal segment is composed of segments 7-10 and has four distinct rows of posteriorly projecting spines.

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EVIDENCE OF POLYGYNOUS RED IMPORTED FIRE ANTS (HYMENOPTERA: FORMICIDAE) IN SOUTH CAROLINA

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Polygynous red imported fire ant populations have the potential for greater economic and environmental damage than the monogyne form because polygyne mound and population densities are two to three times greater than monogyne mound and population densities (Lofgren & Williams 1984; Vinson & Sorensen 1986; Porter 1992; Macom & Porter 1996). In addition to polygyne mound diameters being slightly smaller than monogyne mounds (Porter 1992), polygynous workers are smaller, lighter in color, and less aggressive toward neighboring mounds. Polygyne queens lay fewer eggs, weigh less than monogyne queens (Greenberg et al. 1985), and produce fewer reproductives (Vinson & Sorensen 1986). Polygynous colonies reproduce both via mating flights and budding but reproduce primarily by budding (Vargo & Porter 1989). Polygynous colonies, due to their abundance and competitive pressure, have a greater capacity to eliminate arthropods, including native ant species (Porter & Savignano 1990), plants, and vertebrates (Porter et al. 1991). The purpose of this study is to document the overall presence of polygynous colonies of *S. invicta* in the state of South Carolina. This information may be used to improve the effectiveness of red imported fire ant management because polygyny may affect the type and duration of control needed and pesticide application rates (Porter et al. 1991).

Seven counties across five edaphic regions of South Carolina (Blue Ridge, Piedmont, Southeastern Plains, Middle Atlantic Coastal Plains and Southern Coastal Plains) were evaluated during the fall of 1999 and spring of 2000 for the likelihood of possessing polygynous red imported fire ant colonies. *S. invicta* queens were collected from roadsides and pastures in five South Carolina counties (Pickens, Anderson, Aiken, Richland, and Beaufort) using high mound densities (200+ mounds/ha) as an indicator of polygyny. Horry and Colleton counties were also surveyed but mound densities were too low to suspect polygynous colonies were established there.

Two to six colonies were sampled from each site suspected of polygyny. Queens were collected from the surface of overturned mounds or by excavating colonies. Excavated colonies were placed

into 18.9-L buckets with a 7.6-cm Fluon® band at the top. The drip-flotation method was used to remove queens from the soil (Banks et al. 1981). All red imported fire ant queens were stored in 70% alcohol until they were dissected to confirm that each queen had mated and established within the colony. Dissection was completed using the technique of Glancey et al. (1973) to identify the presence of both an enlarged sperm-filled spermatheca and degenerated wing muscles. In colonies with multiple dealates, up to five randomly selected queens were dissected.

This study shows polygynous red imported fire ants are present in South Carolina (Fig. 1). Beaufort was the only county sampled that did not have multiple inseminated queens. Out of the remaining fifteen colonies sampled from four counties, thirteen colonies from a total of four counties (Pickens, Anderson, Aiken and Richland) had multiple inseminated queens with degenerated

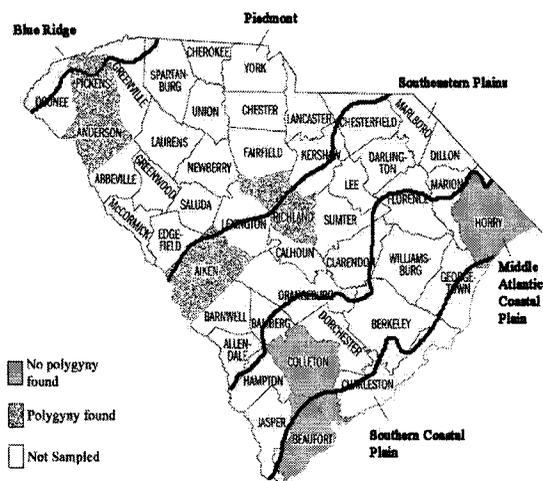


Fig. 1. South Carolina map showing counties sampled for polygynous red imported fire ant colonies. Counties in the Blue Ridge, Piedmont and southeastern plains had polygynous colonies while only monogynous colonies appeared to be in the Middle Atlantic and southern Coastal Plains counties. This map is adapted from an EPA ecoregion map and the U.S. census county map.

wing muscles. At the time of sampling, our results indicated polygyny was found in the Blue Ridge, Piedmont and southeastern plains of South Carolina. Observations in two coastal counties suggested that polygyne red imported fire ant may not be present in the Middle Atlantic or southern coastal plains. Further study is warranted to determine the extent of polygyny throughout the state of South Carolina.

We would like to thank Jack Keener, Marion Barnes, Dr. Jeff Isley, Jodi Bock and TCI International (Aiken Co. Fish Farm) for assistance in locating potential polygynous sites. We would also like to thank Clyde S. Gorsuch and Craig Allen for their assistance. This article is technical contribution No. 4829 of the South Carolina Agricultural Experiment Station.

SUMMARY

Polygynous red imported fire ant colonies were found in the western and central regions of South Carolina. Additional studies should be conducted to more precisely determine the extent of polygyny in the state of South Carolina.

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STATUS OF EUONYMUS SCALE IN MASSACHUSETTS
FOURTEEN YEARS AFTER RELEASE OF *CHILOCORUS KUWANAE*
(COLEOPTERA: COCCINELLIDAE)

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Chilocorus kuwanae (Silvestri) (Coleoptera: Coccinellidae) was imported to the United States from Korea in the 1980s and established in the Washington, D.C. area for control of euonymus scale, *Unaspis euonymi* (Comstock) (Homoptera: Diaspididae) (Drea & Carlson 1987). Limited releases of this population were made in Massachusetts in 1988 and 1989. In 1990, additional adults of *C. kuwanae* were collected near Beijing, China, and used to make a larger set of releases in New England from 1991 to 1994 (Van Driesche et al. 1998a). Widespread establishment occurred (Van Driesche et al. 1998a) and studies indicated that this beetle's presence was correlated with reductions in euonymus scale populations at the level of local study sites that received releases of the beetle (Van Driesche et al. 1998b). The proportion of shrubs heavily infested by euonymus scale at one 50-ha apartment complex with over 100 euonymus plants scattered over the property declined from 46% to 14% between 1991 (year of release) and 1995 (last year of study) (Van Driesche et al. 1998b).

County by county surveys in Massachusetts of euonymus plants in the public landscape (plantings around commercial buildings, institutions, parks or apartment complexes) were conducted from 1989 to 1994. Each year, nine to eleven counties were surveyed over the entire state (except Boston and the islands of Nantucket and Martha's Vineyard), with 475 to 1107 plants per year examined and classified as none, light, medium, or heavy scale infestation (see Van Driesche et al. [1998c] for definitions of categories). The presence of *Chilocorus* sp. beetles on plants was also recorded. Nearly all (>99%) of these were *C. kuwanae*, but a few were the native species *Chilocorus stigma* (Say). For the six year study period, the percentage of shrubs in the heavily infested category averaged 17.9% ($n = 5662$), ranging from 9.4 to 24.6% (Van Driesche et al. 1998c). For just the two years (1989-1990) of the project before the new biological control agent became widespread at the landscape level, 19.2% of plants had heavy scale infestations.

In 2002, we again conducted a survey of euonymus scale on landscape shrubs in Massachusetts using the same protocols as in Van Driesche et al. (1998c) to measure the percentage of euonymus plants with heavy euonymus scale infestations. Our intention was to compare this value to the average from the 1989-1994 period to see if infestation levels had changed. Between late August and

mid October (the same time period as in the earlier surveys), 1119 euonymus plants were randomly located in the public landscape (in eleven counties, approx. 100 plants per county, with approx. three communities examined per county).

In 2002, the percentage of plants in scale infestation categories were as follows: no scale—38.5% (431/1119 plants), light infestation—38.8% (434/1119), medium infestation—11.1% (124/1119), and heavy infestation—11.6% (130/1119). Only plants in the heavy infestation category are at increased risk of dying over a 1 yr period (Van Driesche et al. 1998c) and so it is change in number of shrubs in this category that is of greatest importance. The percentage of plants with heavy scale infestations in 2002 (11.6%), while within the range of values seen in the 1989-1994 surveys, was significantly lower than the average value (17.9%) for that period ($\chi^2 = 26.03$, $df = 1$, $P < 0.005$). This is a 35% decrease in the proportion of landscape plants in the heavily infested group (compared to the 1989-1994 average) and a 39.6% drop from the two survey years (1989-1990 before the widespread release of *C. kuwanae* in the area).

When data were grouped into coastal (Barnstable, Plymouth, Bristol, Essex) versus inland counties (Worcester, Franklin, Hampden, Berkshire, Hampshire, Norfolk, and Middlesex), coastal counties had a significantly lower percentage of heavily infested plants (8.5%, 35/410) than did inland counties (13.4%, 95/709) ($\chi^2 = 6.08$, $df = 1$, $P < 0.025$). Also, coastal plants with heavy scale infestations were significantly more likely to have *C. kuwanae* beetles on the plants when surveyed (57%, 20/35) compared to inland counties (38%, 36/94) ($\chi^2 = 3.95$, $df = 1$, $P < 0.05$). Coastal counties have milder winter temperatures and this may favor survival of this predacious beetle and the associated scale reduction. Indeed, the greatest difference among counties in the survey was between the most coastal county (Barnstable, which is Cape Cod, with 4.1% [4/98] plants with heavy scale infestations and 50% [2/4] of such plants with *C. kuwanae* present) versus the most inland, hilly county (Berkshire, with 19.8% [20/101] plants with heavy scale infestations and 0% [0/20] of these plants with *C. kuwanae* present).

The decline in proportions of euonymus plants heavily infested with scale in the earlier evaluation compared to the survey in 2002 was correlated with increases in the frequency with which the predatory beetle *C. kuwanae* was found on euonymus plants in 2002 compared to previously

published values for 1992-1994 (for MA + RI + CT, Van Driesche et al. 1998a). The percentage of plants on which *C. kuwanae* beetles were found increased in all categories with scale: light infestation from 6% (84/1401) to 15% (65/434), medium infestation from 12.5% (93/745) to 37.9% (47/124), and heavy infestation from 26% (259/995) to 43.1% (65/130), but not for uninfested plants (from 1% [17/1702] to 0.2% [1/431]). Increases in rates of detection of *C. kuwanae* were significant for plants in all three categories of scale infestation: light ($\chi^2 = 36.6$, $df = 1$, $P < 0.005$), medium ($\chi^2 = 50.8$, $df = 1$, $P < 0.005$), and heavy ($\chi^2 = 17.5$, $df = 1$, $P < 0.005$), but not for uninfested plants ($\chi^2 = 2.52$, $df = 1$, $P < 0.25$).

Van Driesche et al. (1998c) speculated that if the percentage of landscape plants with heavy scale infestation should decline eventually by the same degree (69%) as seen in the project's study plots (Van Driesche et al. 1998b), then the annual savings to southern New England (MA, RI, CT) from the introduction of *C. kuwanae* would be \$436,154. Data from our 2002 survey suggest that substantial, though smaller, savings may have been the actual result. Taking values for the estimated number of euonymus plants in MA (821,000) and increased annual mortality rate of heavily infested shrubs compared to uninfested shrubs (12.1 vs. 3.0%) from Van Driesche et al. (1998c) and the observed decrease in the percentage of MA plants in the heavy scale infestation category (from 19.2% for 1989-1990, the pre-introduction period to 11.6% in 2002), we calculated that within this population of plants, mortality has decreased from 14,345 to 8667 plants in MA annually. If we assume that owners were to replace dead plants with the same species and that replacements for these plants were still valued at \$22.50 (the figure in Van Driesche et al. 1998c), this would result in savings of \$127,756, which when doubled (as per Van Driesche et al. 1998c) to represent all of southern New England, gives a value of \$255,512 (compared to the figure in Van Driesche et al. 1998c of \$436,154). To have realized the full projected benefits, the percentage of plants in the landscape that were heavily infested with scale would have had to have fallen to 6.0%, a value lower than that actually observed (11.6%) in 2002. However, because the proportion of plants in coastal areas with heavy scale infestations did fall further (to 8.5% in MA coastal counties), our analysis may underestimate benefits for

southern New England because MA values are applied to CT and RI, which because they are predominantly coastal, may have lower heavy scale infestation rates, more similar to those of just the coastal counties of MA. But data are not available for such an analysis.

We conclude that this project is now returning 2.1 fold in benefits annually (based on values in Van Driesche et al. 1998c and a 35% decline in heavily infested plants) given the amount of money originally invested in the project. These benefits are accumulating with each subsequent year, with no further cost. These savings suggest that this was a successful biological control project.

SUMMARY

The percentage of euonymus plants in the landscape in Massachusetts with heavy euonymus scale infestations has dropped from 19.2% in 1989-1990 to 11.6% in 2002, a 35% decline. For euonymus plants with scale, the proportion of plants on which *C. kuwanae* was present increased between the two survey periods, with this predator being detected at 43.1% of all plants with heavy scale infestation. The percentage of plants infested with euonymus scale was lower in coastal vs. inland counties. Numbers of plants in Massachusetts dying due to scale infestations have been reduced by nearly 6000 per year, with cost savings of at least \$127,756.

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PEÑA, J. E., J. L. SHARP, AND M. WYSOKI (eds.). 2002. Tropical Fruit Pests and Pollinators: Biology, Economic Importance, Natural Enemies and Control. CABI Publishing. Oxon, UK. 430 pp. ISBN 0-85199-434-2. Hardcover. \$149.00.

This book is a series of chapters on the arthropod pests, natural enemies and pollinators of ten different tropical fruits as well as five "minor" fruits. Also included is a final chapter on quarantine treatments for exported fruits. The information is worldwide in scope; the authors are researchers from China, Thailand, Australia, Israel, Kenya, Uganda, South Africa, Brazil, Mexico, Puerto Rico and the United States. Being a tropical fruit enthusiast (I like to eat them), I was eager to start reading this book focusing on other things that eat them too!

The most inclusive chapters in the book are about the pests of avocado, citrus and bananas, followed by litchi/longan, passionfruit, mango, *Annona*, papaya, pineapple and guava. There is also a discussion of the pests of durian, carambola, Barbados cherry (or acerola), mangosteen and rambutan, the minor tropical fruits. Since production of exotic tropical fruit outside their area of origin, both commercially and as backyard fruits, is increasing, it is important to find the information about the existing and potential pest problems.

The introduction (chapter 1) points out our lack of knowledge about tropical fruits as opposed to temperate fruits. Insect sampling protocols, population studies and economic impact of pests are poorly understood or unknown for most tropical fruit pests. This makes implementation of integrated pest management strategies difficult. However, some strategies, such as biological control, have great potential because of the perennial nature of many of the tropical fruit crops. Each chapter starts with a brief description of the fruit crop, cultivation characteristics and production and use information when appropriate. Control methods including cultural control, biological control and chemical control are included. The importance of insect pollinators and the consideration of the impact of pest management strategies on these insects is stressed.

Chapter 2 on pests of bananas is organized under subheadings of pests of the different plant parts (i.e., rhizome and pseudostem, foliage, fruits and flowers). This general organization was also used for chapter 4 (mango), chapter 5 (papaya), and chapter 7 (*Annona*). I liked this layout for diagnostic purposes. I did not like that family affiliations, in some cases, were not included. Chapter 3 on pests of citrus, chapter 9 on guava and chapter 12 on passion fruit were organized under the subheadings of key pests and other pests. I particularly liked table 3.1 which listed the pest species by geographic region as well as tables 3.2-3.8 which listed the major parasitoids for different insect groups on citrus and their area of origin. Other chapters had different organizational

schemes. For example, chapter 8 on avocado used a taxonomic hierarchy in discussing the insect pests. Chapter 6 on pineapple was broadly divided into nematode and arthropod pests. Table 6.2 noted the geographic distribution of the key nematode pests as did table 6.3 for the arthropods. Particularly helpful was the information of the part of the plant attacked and an indicator of the pest status (major, minor) for different growing areas in table 6.3. Chapter 10 discussed the key pests of some minor tropical fruits (durian, mangosteen, rambutan, carambola, and Barbados cherry or acerola).

The book could have profited from more careful editing. For example, there is no rhyme or reason to the layout of the color plates. Some of the pages the order of the numbering of the figures is numerical across rows left to right, others it is numerical down columns and others the order is circular or seemingly random. Also, in the legends for the color plates, sometimes only the common name of the arthropod is given, sometimes the scientific name, other times both. For clarity, it would have been better if both were included when possible, at least for the first plate of a particular species. Plates 1-5 all are of the banana weevil, *Cosmopolites sordidus*, but the legends are banana weevil (plate 1) *Cosmopolites sordidus* (plate 2) and banana weevil (plates 3-5). In many chapters, references cited in the text were omitted from the citations at the end of the chapter. The order and genus of an insect was misspelled (*Tessaritomidae* instead of *Tessaratomidae*). It would have been helpful to have a common organizational structure for all the chapters.

This book would have been better if more figures, either line drawings or black and white photographs of the pests/damage had been included. When a pest species was common to a number of different fruits as are some of the tephritid flies, a lengthy description of the pest could have been included in one chapter and then just referenced in the other chapters.

The authors made a good effort to make this work worldwide in discussion of fruit culture, pests, pollinators and control. I appreciated the inclusion of not only primary literature in the references but also non-refereed publications as well as master's and Ph.D. citations. Even with the editing errors, the information is very easy to read, up to date and complete. This book will be a useful reference for tropical fruit producers and specialists.

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