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Bioecological Studies on the Whiteflies (Hemiptera: Aleyrodidae) of Trinidad and Tobago

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ABSTRACT

Laboratory and field studies were carried out to elucidate the biology and ecology of indigenous species of *Aleurodicus* (Hemiptera: Aleyrodidae) and other aleurodids in Trinidad and Tobago. Data are presented on the lifecycle of three commonly occurring whiteflies in Trinidad (*Aleurodicus cocois* (Curtis), *Aleurodicus pulvinatus* (Maskell) and *Aleurothrixus floccosus* (Maskell)) under constant temperature conditions in the laboratory. Males of all three species generally developed faster than females. *Aleurothrixus floccosus* developed faster than the two *Aleurodicus* spp. and oviposited the highest number of eggs per female. Egg hatch ranged from 85% in *A. floccosus* to 88% in *A. cocois*. Distinguishing features of the three species are described. During field surveys, several *Aleurodicus* species known to occur in Trinidad were encountered together with two undescribed aleurodicine species (*Aleurodicus* sp. and *Lecanoideus* sp.). One new country record (*Aleurotrachelus atratus* Hempel) and 13 new host plant records were also established. Contrary to expectations, the spiralling whitefly *Aleurodicus dispersus* Russell was not found either in Trinidad or Tobago. Whiteflies and their natural enemies were found throughout the year. A range of natural enemies appeared to keep whitefly populations in check. *Nephaspis* spp. were predominant among the predators, while *Encarsiella* spp. and *Encarsia* spp. were predominant among the parasitoids. Natural epizootics of the entomopathogenic fungus *Aschersonia aleyrodalis* Webb were encountered only under persistent high humidity conditions.

Key words: Whitefly, Aleyrodidae, Aleurodicinae, Aleyrodinae, *Aleurodicus cocois*, *Aleurodicus pulvinatus*, *Aleurothrixus floccosus*, bioecology, Trinidad and Tobago.

INTRODUCTION

Many species belonging to the genus *Aleurodicus* (Hemiptera: Aleyrodidae: Aleurodicinae) are native to the New World tropics, occurring in Central and South America and the Caribbean. Several species in this genus have also become invasive, notably *Aleurodicus cocois* (Curtis) in Barbados (Cock 1985), *Aleurodicus dugesii* Cockerell in the United States (Zolnerowich and Rose 1996) and *Aleurodicus pulvinatus* (Maskell) in the Caribbean (Martin and Watson 1998). However, by far the most devastating is the spiralling whitefly, *Aleurodicus dispersus* Russell. This species was accidentally introduced to the Canary Islands in 1962 and to Hawaii in 1978 (Russell 1965; Paulson and Kumashiro 1985). Over the next two decades it spread widely to all the islands of the Pacific as well as to Asia, Australia and West Africa (Waterhouse and Norris 1989; Wijesekera and Kudagama 1990; Kajita *et al.* 1991; Akinlosotu *et al.* 1993; Wen *et al.* 1994; Palaniswami *et al.* 1995; Alam *et al.* 1997; Lambkin 1999).

A considerable amount of literature exists on the biology of *Aleurodicus* spp., pertaining mostly to areas where *A. dispersus* has been introduced (Kumashiro *et al.* 1983; Waterhouse and Norris 1989; Wen *et al.* 1996; D'Almeida *et al.* 1998; Mani and Krishnamoorthy 2000). The present study was therefore undertaken to elucidate the biology of whitefly, particularly *Aleurodicus* spp. and their natural enemies in their native habitat in Trinidad since little is known beyond records of their presence on a few host plants (Mound and Halsey 1978). Even the presence of *A. dispersus* in Trinidad was debatable: this species was not reported from Trinidad in Mound and Halsey's (1978) catalogue of whitefly. However, natural enemies sent from Trinidad to Hawaii in 1979/80 (reportedly collected on *A. dispersus*) (Gordon 1982) were effective in controlling the whitefly not only in Hawaii, but also elsewhere where *A. dispersus* was accidentally introduced (Kumashiro *et al.* 1983; Waterhouse and Norris 1989; D'Almeida *et al.* 1998).

The study reported here formed part of a larger project, aimed at evaluating the predatory coccinellid, *Nephaspis bicolor* Gordon (Coleoptera: Coccinellidae), as a biological control agent

of Aleyrodidae, particularly *Aleurodicus* spp. (Lopez 2003; Lopez and Kairo 2003). One of the objectives of the study was to resolve the issue of whether *A. dispersus* was present in Trinidad or not. Three whitefly species consistently encountered during the surveys were later used for culturing, and studies on *N. bicolor*. These were *A. cocois*, *A. pulvinatus* (both subfamily Aleurodicinae) and *Aleurothrixus floccosus* (Maskell) (subfamily Aleyrodinae). The biology of the first two species has been little studied (Gondim and Sales 1981; Martin and Watson 1998). Although the woolly whitefly, *A. floccosus*, has been the subject of numerous studies, these have been almost exclusively on *Citrus* spp. hosts (Paulson and Beardsley 1986; Carvalho 1994). The opportunity was therefore taken to investigate the biology and ecology of these species. The field surveys aimed to establish the identity and host range of *Aleurodicus* spp. and other Aleyrodidae present in Trinidad and Tobago, and to obtain data on their population dynamics. Laboratory studies were aimed at elucidating the developmental and reproductive biology of *A. cocois*, *A. pulvinatus* and *A. floccosus*.

MATERIALS AND METHODS

Field studies

Trinidad and Tobago has two seasons: rainy season from June to December and dry season from January to May. The field surveys in Trinidad were begun in February 1996 and concluded in July 1997, thus encompassing two dry seasons (1996 and 1997) and one rainy season (1996). Surveys in Tobago were carried out in July and December 1996 and March and May 1997.

The areas surveyed in Trinidad were divided into eight zones for recording purposes (Fig. 1). Six areas were surveyed in Tobago, designated Zone 9. Zones 1, 3, 4 and 6, which had heavier infestations of *Aleurodicus* spp., were surveyed more regularly than the other zones.

At each survey location, potential host plants of *Aleurodicus* spp., namely guava (*Psidium guajava*), coconut (*Cocos nucifera*) and other palms, seagrape (*Coccoloba uvifera*), mango (*Mangifera indica*), citrus (*Citrus* spp.), cassava (*Manihot esculenta*), avocado

* deceased

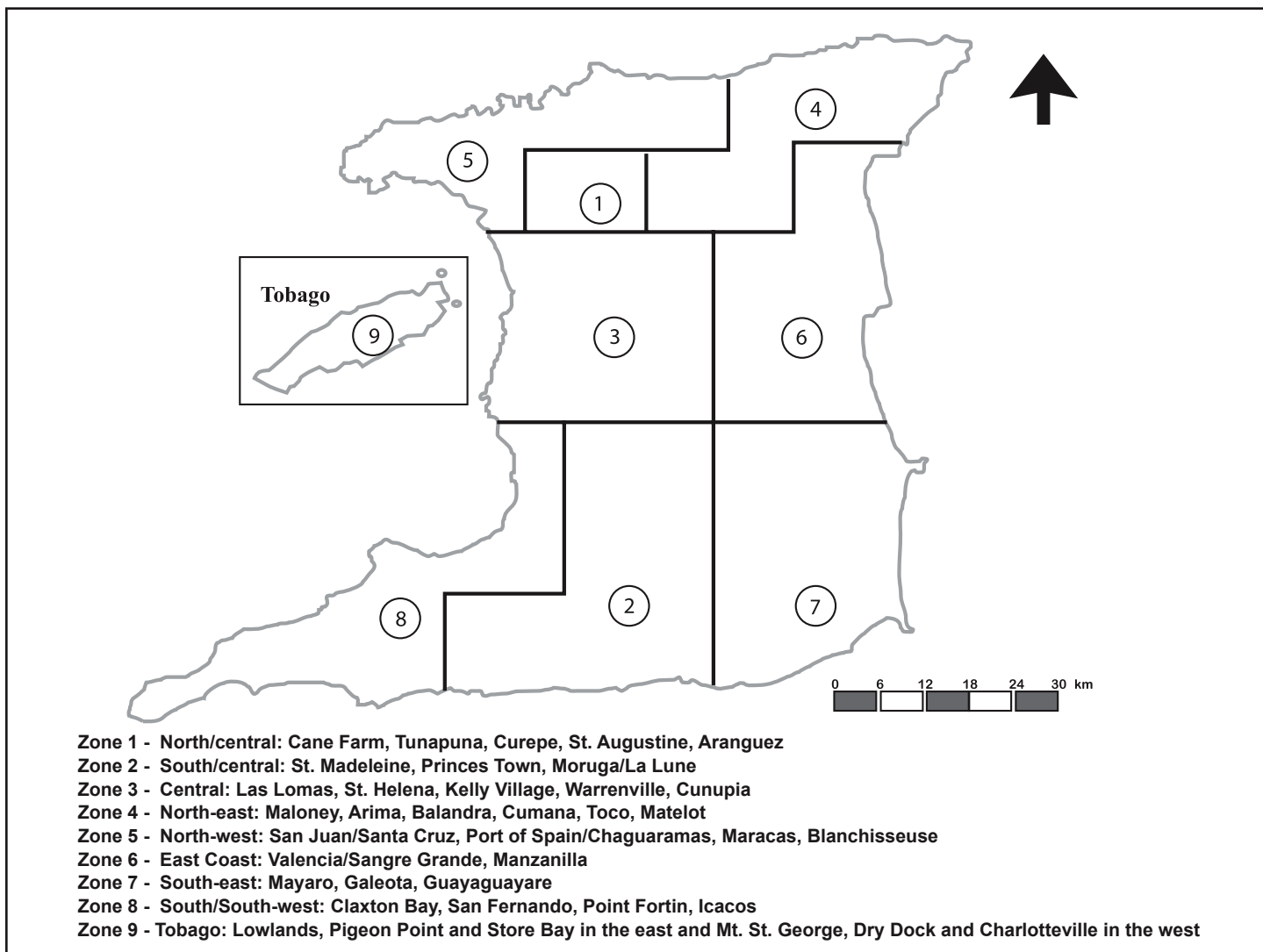


Fig. 1. Map of Trinidad and Tobago (inset) indicating areas surveyed under Zones 1-9.

(*Persea americana*), ficus (*Ficus benjamina*) and banana (*Musa* sp.), as well as surrounding trees/plants, were examined for the presence of whitefly and their natural enemies. When whitefly were encountered, an assessment of their population level was carried out using a qualitative scale as follows:

0 = no infestation;

1 = low infestation, <30% leaf surface/leaves infested;

2 = medium infestation, 30-70% leaf surface/leaves infested and

3 = high infestation, >70% leaf surface/leaves infested.

Associated natural enemies (*Nephaspis* spp. and other predators, parasitoids and microbial control agents) were also recorded. Wherever possible, samples of whitefly pupae were collected and brought to the laboratory for assessment. Coccinellid larvae/pupae in the sample were collected and reared for adults as well as for natural enemies (parasitoids/diseases). Percentage parasitism of whitefly was estimated by recording the number of parasitized pupae in batches of 100 randomly selected pupae. This was based on the colour of pupae, which are often covered in white wax and are black (pupa of parasitoid) or clear white (all contents fed upon) when parasitized but are pale greenish or yellow in unparasitized insects. At each location, 300-500 pupae were assessed and the average calculated to obtain percentage parasitism for that location on that sampling date.

Morphological characteristics of the live pupae (e.g. colour, size, shape of wax strands) of several whitefly species were recorded from a number of hosts. Field-collected leaf samples bearing the pupae were preserved in glass vials with 70% alcohol and sent for identification. Slides of pupae from several other hosts/locations were also prepared following the method outlined by Martin (1987). When authoritatively identified reference material was received, comparisons were made with the slide-mounted specimens to establish the identity of the whitefly.

Laboratory studies

Developmental biology

Four coconut plants, 40-50 cm tall each and with three open fronds, were used for the study on *A. cocois*. The fronds were examined carefully and all contaminants (e.g. scales, mealybugs and whitefly) removed. They were then wiped clean with a moist cloth and allowed to dry. The plants were placed on light frames in controlled-temperature laboratories (CT Rooms) maintained at $26 \pm 2^\circ\text{C}$. Each light frame consisted of a bank of 4-6 fluorescent lights and 2-4 incandescent bulbs suspended 20-30 cm above the cages. The lighting regime used was 12 h light and 12 h dark. Mated *A. cocois* adults were released on the middle leaf under sleeve cages for oviposition and were removed 24 h later. Egg size (length and

width) was measured for 30 randomly selected eggs. Observations were recorded daily on egg hatch. Once the eggs hatched and the crawlers had settled, 15-30 individuals were numbered on each plant and observed daily for change of instar, pupation and adult emergence. The size (length and width) of 30 randomly selected nymphs was measured immediately after change of instar and at pupation. The presence of moulted skin on the dorsal surface of the nymph indicated that the insect had changed instars overnight. This was recorded and the moulted skin was removed. The 4th instar was considered to have become a pupa when it stopped growing and retained a constant size over a 2-day period. By this time, the entire body usually became coated with a white powdery wax, and the wax patterns / strands that characterized each species also became distinct.

Four seagrape and guava plants were similarly prepared and used for studies on *A. pulvinatus* and *A. floccosus*, respectively. The plants, each 20-30 cm tall, were placed inside 40 cm x 40 cm x 40 cm mesh cages. All other experimental details and observations were the same as for *A. cocois* above.

Reproductive biology

Manipulation of whitefly adults with an aspirator often resulted

in high mortality. Therefore, to study the reproductive biology, five plants with leaves harbouring known numbers of pupae (approximately 15 per leaf) were individually isolated in sleeve cages prior to adult emergence. After emergence, the adults were allowed to remain on the same leaf and observed daily to record preoviposition period and mortality. Dead adults were carefully removed every day and their sex recorded. When all the adults were dead, the number of females per leaf was counted together with the number of eggs oviposited. Percent egg hatch was calculated based on the total number of eggs laid and total numbers hatched.

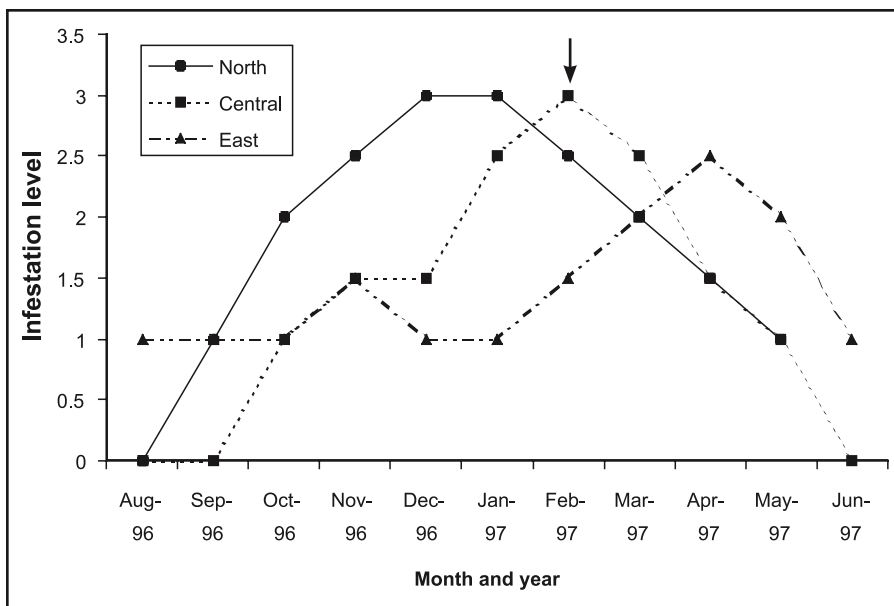
RESULTS

Field studies

Species of Aleyrodidae and their host plants recorded during field surveys are presented in Table 1. Several *Aleurodicus* spp. were encountered, but *A. dispersus* was not found on any of its known, common hosts such as guava, seagrapes and cassava. On guava, *A. maritimus* was the predominant species and *A. pulvinatus* was encountered occasionally, while *A. floccosus* was often found in association with both species. Seagrape was the main host plant for *A. pulvinatus*. Coconut and other palms, particularly the Manila palm, *Veitchia merrillii*, harboured mainly *A. cocois*, at least two

Table 1. Aleyrodidae and their host plants recorded in Trinidad and Tobago.

Species	Host plants	Remarks
<i>Aleurodicus capianga</i> Bondar	Frangipani (<i>Plumeria</i> sp.) Plum (<i>Spondias</i> sp.)	New host record New host record
<i>Aleurodicus cocois</i> (Curtis)	Coconut (<i>Cocos nucifera</i>) Ficus (<i>Ficus benjamina</i>) Manila palm (<i>Veitchia merrillii</i>) Carat palm (<i>Sabal</i> spp.) Bamboo palm (<i>Chrysalidocarpus lutescens</i>)	New host record New host record New host record
<i>Aleurodicus maritimus</i> Hempel	Guava (<i>Psidium guajava</i>) Pigeon pea (<i>Cajanus cajan</i>)	
<i>Aleurodicus pulvinatus</i> (Maskell)	Coconut, Guava Seagrape (<i>Coccoloba uvifera</i>) Tropical almond (<i>Terminalia catappa</i>)	New host record New host record
<i>Aleurodicus trinidadensis</i> Quaintance and Baker	Coconut	
<i>Aleurodicus</i> sp.	Seagrape	Undescribed species
<i>Ceraleurodicus bakeri/moreirai</i> (Bondar)/Costa Lima	Coconut	New host record
<i>Lecanoideus mirabilis</i> (Cockerell)	Ficus Ashoka (<i>Polyalthia longifolia</i>)	New host record New host record
<i>Lecanoideus</i> sp.	Seagrape	Undescribed species
<i>Paraleyrodes urichii</i> Quaintance and Baker	Coconut	New host record
<i>Paraleyrodes</i> sp.	Coconut, Manila palm, Bamboo palm, Carat palm	
<i>Aleurothrixus floccosus</i> (Maskell)	Guava, Citrus (<i>Citrus</i> spp.) Pommecythere (<i>Spondias dulcis</i>)	New host record
<i>Aleurotrachelus atratus</i> Hempel	Coconut	New host and country record
<i>Aleurotrachelus trachoides</i> Back	Frangipani	New host record
<i>Aleurotrachelus</i> sp.	Coconut, Manila palm, Bamboo palm, Carat palm	
<i>Bemisia tabaci</i> biotype b	Pumpkin, Cabbage	



↓ = the first time that *Encarsiella noyesi* was encountered at this location.

Fig. 2. Infestation levels of *Aleurodicus cocois* on coconut at three locations in Central (Zone 3) and East Trinidad (Zone 6) and on Manila palm in North Trinidad (Zone 4).

species of *Paraleyrodes* (*Paraleyrodes* sp. and *P. urichii* Quaintance and Baker) and three species of *Aleurotrachelus* (*Aleurotrachelus* sp., *A. atratus* Bondar and *A. trachoides* Back). Several *Aleurodicus* species known to occur in Trinidad were recorded, together with two undescribed aleurodicine species. One new country record and several new host plant records were established (Table 1).

Whiteflies and their natural enemies were found throughout the year. Three factors, either alone or in conjunction with each other, appeared to play an important role in the observed population patterns of *Aleurodicus* spp. These were the phenology of host plants (populations on guava), local weather conditions (populations on coconut and seagrape) and the natural enemy complex (populations on all hosts / host plants). On guava, populations of *Aleurodicus* spp. and *A. floccosus* normally increased whenever there was new flush growth on the plants following periods of rainfall. During the dry season, however, new flush growth occurred only on trees that had a regular supply of water (e.g. near drains). Hence these species were encountered throughout the year at different locations. However, factors other than plant phenology were apparently more important in the case of *A. cocois* on coconut and other palms and *A. pulvinatus* on seagrape. During the rainy season, these species were present in low numbers even though the plants had new fronds and leaves. During dry periods, however, their populations increased very rapidly, indicating that lower rainfall and/or relative humidity favoured the development of these species.

Each generation of the whitefly took about one month for completion, and thus there were more than 12 overlapping generations annually. Peak populations occurred at different periods for different species e.g. populations of *A. cocois* and *A.*

pulvinatus on coconut and seagrape, respectively, remained low during the rainy season and peaked in the dry season. The influence of weather was particularly evident for *A. cocois* during the transition period between the rainy/dry season at two locations. Populations of this whitefly species in Central and North Trinidad began to increase in October / November 1996 when the rains declined and peaked around January / February 1997 (Fig. 2). On the other hand, persistent rains until January / February 1997 along the East Coast caused populations to remain low until March and then increase rapidly during April / May. At all locations, natural enemies caused a rapid decline in *A. cocois* populations within 4-6 weeks of the population peak, i.e. by April / May in Central and North Trinidad and by June in the East (Fig. 2). Population peaks of *A. maritimus*, *A. pulvinatus* and *A. floccosus* on guava, on the other hand, were related to the appearance of new flush growth, and peaked at different times on different trees (Fig. 3).

A range of natural enemies (mainly parasitoids and predators) accompanied even incipient whitefly populations. These appeared to be responsible for the rapid decrease or even annihilation of populations within a short period, often in just a few days to a few weeks. *Nephaspis* spp. were predominant among the predators and were encountered at most sites even when whitefly populations were low. The other predators (syrphids, chrysopids, spiders and ants) were more sporadic in distribution and numbers.

A total of fifteen species of parasitoids, including three hyperparasitoids, was recorded from various aleyrodid species and a summary based on Lopez and Kairo (2003) is provided in Table 2. Of these, one species each belonged to Platygasteridae (*Amitus*) and Eulophidae (*Entedononecremnus*), two to Encyrtidae (*Metaphycus*) and the remaining eight species to Aphelinidae (*Encarsiella*, *Encarsia*). Three species of the hyperparasitic genus *Signiphora* (Signiphoridae) were found at three locations; however, this group was not encountered in areas where high levels of whitefly

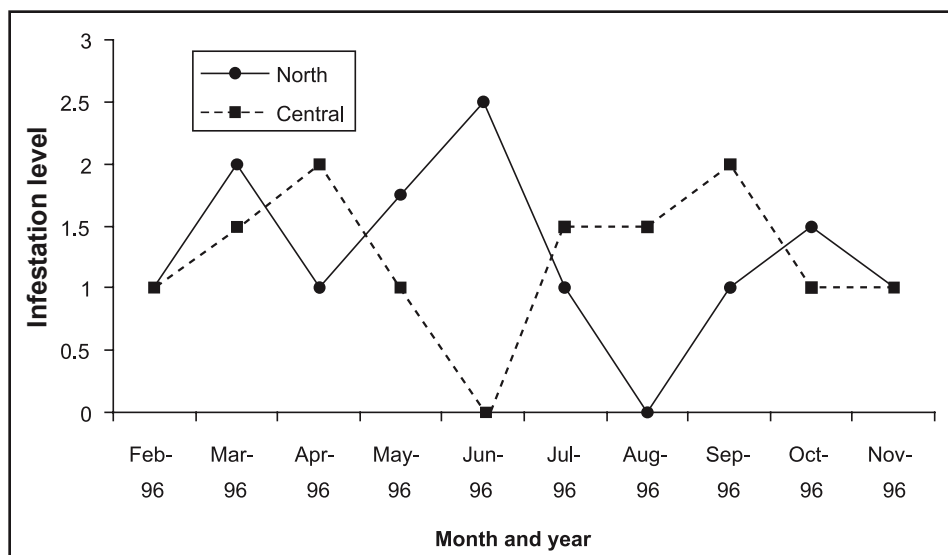


Fig. 3. Infestation levels of *Aleurodicus maritimus* on guava in North (Zone 1) and Central (Zone 3) Trinidad.

Table 2. Parasitoids of Aleyrodidae recorded in Trinidad and Tobago (based on Lopez and Kairo, 2003).

Species	Ex: host	Host plant
<i>Encarsia cubensis</i> Gahan	<i>Aleurothrixus floccosus</i>	Guava
<i>Encarsia guadeloupae</i> Viggiani	<i>Aleurodicus maritimus</i> <i>A. cocois</i> <i>A. pulvinatus</i> <i>Lecanoideus mirabilis</i>	Guava Manila palm Seagrape Ashoka tree
<i>Encarsia hispida</i> DeSantis	<i>Aleurothrixus floccosus</i>	Guava
<i>Encarsia</i> sp. nr. <i>meritoria</i> Gahan Sp. A.	<i>A. maritimus</i> <i>A. cocois</i> <i>Aleurothrixus floccosus</i>	Pigeon pea, Guava Manila palm <i>Spondias dulcis</i> , <i>Citrus</i> , Guava, <i>Pimenta</i> sp.
<i>Encarsia</i> sp. nr. <i>meritoria</i> Gahan Sp. B.	<i>A. cocois</i> + <i>Paraleyrodes</i> sp. <i>A. maritimus</i>	Coconut Guava
<i>Encarsia</i> sp. nr. <i>variegata</i> Howard	<i>Aleurothrixus floccosus</i>	Guava
<i>Encarsiella</i> sp. D.	<i>A. cocois</i> <i>A. maritimus</i> <i>A. pulvinatus</i>	Coconut Guava, Pigeon pea Seagrape
<i>Encarsiella noyesi</i> Hayat	<i>A. cocois</i> <i>A. maritimus</i> <i>A. pulvinatus</i>	Coconut Guava Seagrape
<i>Entedononecremnus</i> sp.	<i>Lecanoideus mirabilis</i>	Ficus
<i>Metaphycus</i> sp. 1	<i>Aleurotrachelus</i> sp.	Coconut
<i>Metaphycus</i> sp. 2	<i>A. cocois</i> <i>A. maritimus</i> , <i>A. floccosus</i>	Coconut Guava
<i>Amitus spiniferus</i> (Brèthes)	<i>A. floccosus</i>	Guava
<i>Signiphora xanthographa</i> Blanchard <i>Signiphora</i> spp.	<i>A. floccosus</i> ? <i>A. cocois</i> <i>Aleurotrachelus</i> sp.	Guava Coconut <i>Capsicum</i> sp.

in shape. The length to width ratios indicated a disproportionate increase in the width from the 1st to the 3rd instars in all three species, resulting in a more circular 3rd instar. All three species gradually regained their oval shape by the pupal stage. All stages of *A. floccosus* were smaller than the equivalent stages of the two *Aleurodicus* species. Eggs, 1st and 2nd instars of *A. cocois* and *A. pulvinatus* were very similar in size; however, during the later instars and the pupa stage, *A. cocois* became larger than *A. pulvinatus* (Table 4). For purposes of comparison, if pupal length and width of *A. cocois* is taken as 1 x 1, then the proportionate length and width of *A. pulvinatus* pupae were 0.87 x 1 and *A. floccosus* 0.56 x 0.58.

Among the several distinguishing morphological features of *A. cocois*, *A. pulvinatus* and *A. floccosus* were ovipositional patterns. Eggs of *A. cocois* were usually laid flat on the leaf surface, in perfect spirals particularly in the first generation on a new leaf. In later generations, this pattern tended to become irregular. The wax in the spirals was made up of thick strands, cut off into chain-like links. An extra layer

populations were consistently encountered, and was apparently not very common.

Natural epizootics of the fungus *Aschersonia aleyrodis* Webb were encountered only on two occasions, the first on *A. floccosus* on guava and the second on *A. cocois* on coconut. Both were in high humidity conditions towards the middle of the rainy season and mostly older infestations on mature leaves were attacked. The fungus first appeared as small creamy white patches, later increasing in size considerably (often achieving 2-3 times the size of the whitefly host) and turning dark red to orange.

Laboratory studies

Developmental biology

The durations of development of the various life stages of *A. cocois*, *A. pulvinatus* and *A. floccosus* in the laboratory are presented in Table 3. For all three species, the egg stage had the longest duration followed by the pupal stage. The woolly whitefly *A. floccosus* developed slightly faster (28.3 days) than *A. cocois* (30.3) and *A. pulvinatus* (32.2 days). Males generally developed faster than females.

Sizes of the four instars and pupa are presented in Table 4. The first two instars were distinctly oval

of wax was deposited around each egg, making it quite easy to distinguish these areas. Each spiral contained 12-26 eggs. In *A. pulvinatus*, first generation eggs on a new leaf were oviposited flat in a very orderly pattern in groups of 10-30 along the midrib and veins of the seagrape leaf. The eggs were placed very close to each other at almost equal intervals and covered with wax made up of characteristic thin strands, broken into fine chain-like links. Like

Table 3. Duration (in days) (mean±SE) of various life stages (males and females combined) of three whitefly species (n = 4 replications) in controlled-temperature (26±2°C).

Life stage	<i>Aleurodicus cocois</i> on coconut	<i>Aleurodicus pulvinatus</i> on seagrape	<i>Aleurothrixus floccosus</i> on guava
Egg	10.5±0.09	10.7±0.27	9.6±0.10
1st instar	3.5±0.24	4.4±0.19	3.3±0.05
2nd instar	3.3±0.32	4.1±0.18	3.3±0.19
3rd instar	3.5±0.13	4.1±0.08	3.2±0.09
4th instar	3.9±0.14	2.3±0.04	3.4±0.15
Pupa	5.7±0.13	6.5±0.22	5.6±0.17
Total duration	30.3±0.14	32.2±0.15	28.3±0.07

Table 4. Sizes (in mm) (mean \pm SE) of various developmental stages of three whitefly species (n = 30 insects).

Life stage	<i>Aleurodicus cocois</i> on coconut	<i>Aleurodicus pulvinatus</i> on seagrape	<i>Aleurothrixus floccosus</i> on guava
Egg			
Length	0.35 \pm 0.003	0.34 \pm 0.003	0.21 \pm 0.002
Width	0.13 \pm 0.002	0.12 \pm 0.001	0.08 \pm 0.001
1st instar			
length (l)	0.39 \pm 0.004	0.36 \pm 0.002	0.28 \pm 0.003
width (w)	0.17 \pm 0.002	0.18 \pm 0.001	0.14 \pm 0.002
ratio l/w	2.29	2.00	2.00
2nd instar			
length (l)	0.50 \pm 0.006	0.50 \pm 0.18	0.34 \pm 0.002
width (w)	0.31 \pm 0.005	0.32 \pm 0.004	0.19 \pm 0.003
ratio l/w	1.61	1.56	1.79
3rd instar			
length (l)	0.80 \pm 0.005	0.74 \pm 0.005	0.45 \pm 0.004
width (w)	0.61 \pm 0.005	0.57 \pm 0.004	0.30 \pm 0.003
ratio l/w	1.31	1.30	1.5
4th instar			
length (l)	1.17 \pm 0.006	1.03 \pm 0.007	0.68 \pm 0.006
width (w)	0.75 \pm 0.008	0.72 \pm 0.008	0.41 \pm 0.006
ratio l/w	1.56	1.43	1.66
Pupa			
Length (l)	1.30 \pm 0.005	1.13 \pm 0.004	0.73 \pm 0.006
Width (w)	0.80 \pm 0.006	0.80 \pm 0.005	0.46 \pm 0.005
Ratio l/w	1.63	1.41	1.59

A. cocois, the pattern of oviposition on the same leaf in the second generation was haphazard. Thus, nymphs often developed all over the leaf surface, either singly or in small groups. *Aleurothrixus floccosus* also oviposited eggs in a spiral, however, the eggs were usually laid upright or at a slanting angle. When a large number of adults oviposited on a leaf, the spirals often blended together and individual spirals were difficult to distinguish. A granular wax was deposited in an untidy, powdery mass all around the eggs, making them appear as flat, circular, grainy white areas.

The wax patterns on individual instars were also characteristic of each species. There was little or no wax on the first instar of all three species. Second-instar *A. floccosus* developed thin, thread-like wax strands that curled up into a woolly mass as development progressed. The pupae were often covered with a white woolly mat of wax that was several times thicker than the body of the insect (hence the common name 'woolly whitefly'), together with deposits of clear honeydew. In older pupae, the honeydew deposits dried and turned brownish orange as they became contaminated with saprophytic fungi and other organisms. In *A. cocois* and *A. pulvinatus*, the wax pattern began to develop in the late 2nd / 3rd instar. More wax was deposited along the margins of the nymphs as development continued and single shiny filaments were often seen emerging from each compound pore. Fourth-instar *A. cocois* were particularly easy to distinguish since they had a thin layer of wax along the oval outline of the nymphs. When they pupated, the wax strands became thick and curled under, and appeared to radiate out along the margin of the pupa. In *A. pulvinatus*, on the other hand, the wax along the edges of the pupae was very thick. At times, eggs were laid so close together that the pupae in a sibling group appeared to be glued to each other and some of the faster developing nymphs crushed their slow developing siblings. In

addition, most older stages had two small patches, one on each side of the dorsal surface, which grew in size and became darker as the insect continued to develop. At pupation, the two dark patches were quite distinct and easily distinguished this species from others.

Reproductive biology

Data recorded on the reproductive parameters are summarized in Table 5. *Aleurothrixus floccosus* oviposited the highest number of eggs per female (89). Percentage egg hatch ranged from an average of 84.8% in *A. floccosus* to 88.4% in *A. cocois*.

DISCUSSION

Results from the laboratory studies on the life cycle of the whitefly conformed broadly to the previously recorded biology of *A. cocois* on several hosts and that of *A. floccosus* on *Citrus* spp. (Gondim and Sales 1981; Paulson and Beardsley 1986).

Field surveys revealed the presence of several previously recorded species from Trinidad and Tobago (Mound and Halsey 1978). Thirteen new host records, two new, undescribed species and one new country record were established. *Aleurodicus dispersus* was not found on any of its known hosts, confirming that this species does not occur on Trinidad and Tobago. Several other

Aleurodicus species were found, and it is likely that *Nephaspis indus* Gordon, reportedly collected on guava and coconut (Gordon 1982) was probably feeding on *A. maritimus* and/or *A. pulvinatus* and *A. cocois*, respectively. Of particular interest was the high level of adaptation exhibited by *A. cocois*, *Aleurotrachelus* spp. and *Paraleyrodes* spp. to the Manila palm, which is not native to Trinidad.

Under field conditions, a range of bioecological factors contributes to population levels of whitefly and their management. In several countries, humidity and/or temperature appeared to be important environmental parameters influencing the population dynamics of more than one species of *Aleurodicus*. In the Canary Islands, *A. dispersus* populations were distributed mostly along the coastal regions of Tenerife, Lanzarote and Gran Canaria (Manzano *et al.* 1995). Surveys for *Aleurodicus cocois anacardi* Carvalho, Arruda and Arruda (considered a food plant specific race of *A. cocois*) on cashew in the state of Ceara, Brazil, indicated that infestations were heaviest in areas with high humidity (coastal region) and decreased steadily as the relative humidity decreased with increasing distance from the coast (Melo and Cavalcante 1979). In Benin, D'Almeida *et al.* (1998) found that high humidity was conducive to the development of the immature stages of the exotic *A. dispersus*; however, heavy rainfall resulted in "wash down" of adults. Initially, very high populations of *A. dispersus* declined 80% in the three years following the presence of parasitoids. In India, where *A. dispersus* was introduced in the late 1990s, both temperature and humidity played a role in regulating the whitefly on guava in the absence of specific natural enemies (Mani and Krishnamoorthy 2000). However, in the presence of the parasitoid *E. guadeloupa* on banana, *A. dispersus* populations declined from 116.9 per 25 cm² leaf area in March 2000 to 1.1 per 25 cm² leaf area

Table 5. Reproductive biology of three whitefly species (mean \pm SE; n = 5 replications) in laboratory culture.

Parameter	<i>Aleurodicus cocois</i> on coconut	<i>Aleurodicus pulvinatus</i> on seagrape	<i>Aleurothrix floccosus</i> on guava
Preoviposition period	2.8 \pm 0.37	2.6 \pm 0.25	1.6 \pm 0.25
Mean no. of eggs / female	35.7 \pm 4.33	41.5 \pm 5.07	89.1 \pm 7.61
Longevity of female	6.8 \pm 0.58	7.0 \pm 0.32	12.0 \pm 1.14
Mean no. of eggs / female / day	9.1 \pm 0.95	9.5 \pm 0.94	8.7 \pm 0.67
% egg hatch	88.4 \pm 2.65	87.7 \pm 3.10	84.8 \pm 2.52

in December 2001, with parasitism levels reaching 95.7% (Mani *et al.* 2004).

In Hawaii, natural enemies, rainfall and temperature were significant in regulating *A. dispersus* populations (Kumashiro *et al.* 1983). Studies on the performance of *N. indus* and *Encarsia ?haitiensis* Dozier in two distinct ecological zones revealed that the predator performed best in the lowlands where temperatures were higher and rainfall lower. It remained in high host density areas, with limited dispersal until host numbers declined. The parasitoid density, on the other hand, was high in both lowlands and highlands even when whitefly populations were low. This indicated either a lower food requirement or higher searching ability, allowing the parasitoid to thrive at lower host densities. It was concluded that the parasitoid was adaptable to both highland and lowland conditions (Kumashiro *et al.* 1983). In Costa Rica, a qualitative analysis of temperature and humidity indicated no effect on the population fluctuation of *A. dispersus* and its natural enemies; parasitoids, on the other hand, played an important role in regulating *A. dispersus* populations (Blanco-Metzler and Laprade 2000).

In the present study, whiteflies were recorded throughout the year in almost all areas of Trinidad and Tobago. Distribution patterns observed were either as a result of weather conditions (populations on coconut and seagrape), or phenology of the host plant (populations on guava). On all hosts, a range of natural enemies accompanied even incipient populations and appeared to be responsible for the rapid reduction or total annihilation of populations observed within a few weeks. This explained why the genus *Aleurodicus* has never been considered a serious or economically important problem despite occasional population outbreaks. It was noteworthy that many of the parasitic species (*Encarsia* spp. and *Encarsiella* spp.) attacked a range of aleyrodids belonging to both subfamilies (Aleyrodidae and Aleurodicinae). At least three hyperparasitic species were recorded, however, it seemed unlikely that they played a regulatory role in the overall ecology of the whitefly and their natural enemies since they were recorded infrequently and usually in areas where whitefly populations were low.

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