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Long-term efficacy of *Encarsia dispersa* Polaszek (Hymenoptera: Aphelinidae) for the biological control of *Aleurodicus dispersus* Russell (Hemiptera: Aleyrodidae) in tropical monsoon Australia

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Abstract Introductions of *Encarsia dispersa* Polaszek (Hymenoptera: Aphelinidae) for the biological control of spiralling whitefly, *Aleurodicus dispersus* Russell (Hemiptera: Aleyrodidae), were made directly onto Thursday Island, Torres Strait Queensland, in May 1994. Its efficacy was monitored intermittently for 7 years on 10 *Acalypha wilkesiana* Müll. Arg. (Euphorbiaceae) and two *Terminalia catappa* L. (Combretaceae) plants. Marked declines in whitefly densities were recorded on all hosts approximately 10 months after parasitoid releases. Declines in whitefly densities over the first 2 years were mostly matched with increases in per cent parasitism; these declines generally coinciding with wet seasons, with small resurgences occurring over the first dry season following the first decline. Whitefly densities and per cent leaves infested on *T. catappa*, and on *A. wilkesiana* with flat leaves were low by the latter half of the study. In contrast, *A. wilkesiana* with convoluted leaves seemed to inhibit the parasitoid by providing physical refuges for whitefly nymphs, resulting in higher whitefly numbers with low parasitism, particularly in dry conditions. Ten to 12 years after these initial declines, whitefly densities have remained low. Adults and larvae of *Cryptolaemus affinis* Crotch (Coleoptera: Coccinellidae) and larvae of *Acletoxenus quadristriatus* Duda (Diptera: Drosophilidae) were observed preying on whitefly nymphs during the study. Overall, sampling data suggested that *A. dispersus* was under biological control. It may be prudent to maintain *A. wilkesiana* with convoluted leaves (acting as host refuges) on the Torres Strait islands to retain parasitoid persistence, thereby maintaining controlled and stable populations of *A. dispersus*. In addition, because of the pest's wide host range and the ability for hosts with closed leaf structures, such as *A. wilkesiana* with convoluted leaves, to harbour higher pest numbers, movements of these plants within or out of tropical areas could pose a significant quarantine risk.

Key words *Acletoxenus quadristriatus*, *Cryptolaemus affinis*, host refuge, parasitoid, spiralling whitefly, Torres Strait.

INTRODUCTION

The spiralling whitefly *Aleurodicus dispersus* Russell (Hemiptera: Aleyrodidae) is a tropical pest of a wide range of crops and ornamental plants (Wen *et al.* 1994a; Lambkin 1999; Waterhouse & Sands 2001). The species is believed to have originated in the wet Neo-tropics of Central and South America (Russell 1965; Caballero 1994), but is now almost pan tropical in distribution (Lambkin 1996, 1999; CAB International 2006), occurring also in some subtropical and temperate areas (Russell 1965; Wen *et al.* 1994a; Manzano *et al.* 1995). Since the time that *A. dispersus* assumed pest status (Waterhouse & Sands 2001) seven species of parasitoid (Hymenoptera: Aphelinidae), mainly Neo-tropical in origin, have been recorded from the nymph stage (Kumashiro *et al.* 1983; Blanco-Metzler & Laprade 1998, 2000; Mani & Krishnamoorthy 2002). Only two of these, *Encarsia dispersa* Polaszek (Polaszek *et al.* 2004) and *E. guadeloupae* Viggiani (Hymenoptera: Aphelinidae), have been used widely in biological control programs (Kumashiro *et al.* 1983; Esguerra 1989; Neuenschwander 1996; D'Almeida *et al.* 1998; Chien *et al.* 2000; Lambkin 2004; Mani *et al.* 2004). Until quite recently, *E. dispersa* was known as *E. haitiensis* (Kumashiro *et al.* 1983; Polaszek *et al.* 2004), having been originally collected from Trinidad and imported into Hawaii as a potential biological control agent for *A. dispersus* (Kumashiro *et al.* 1983).

In Australia, *A. dispersus* is currently found in Queensland, where it occurs from Torres Strait, through Cape York Peninsula to as far south as Weipa on the west coast (Lambkin 2004), and along the east coast south to Bargara, near Bundaberg (W Roe unpubl. data 2009), and in the Northern Territory at Darwin (Chin *et al.* 2006) and Humpty Doo (Warren

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2006). Torres Strait forms part of Australia and lies directly north of mainland Queensland. The species was first recorded there on Boigu Island in 1991, a flat mud island lying in the northern sector of the strait, less than 5 km from the southern coast of Papua New Guinea. Within 12 months of its discovery, the biological control agent, *E. dispersa*, was released directly into the field (Lambkin 2004). Despite this, *A. dispersus* continued to progressively spread south, but has remained suppressed by progressive releases of the parasitoid into newly colonised whitefly populations (Waterhouse & Sands 2001). Within 12 months after the initial release of *E. dispersa* on Boigu Island, *A. dispersus* had spread to Thursday Island in the south of the strait, including nearby Hammond, Horn and Prince of Wales Islands, and then shortly after to almost all inhabited islands in Torres Strait (Lambkin 2004). In 1994, parasitoid pupae were collected from Boigu Island and parasitoids were released into whitefly populations on the four southern islands (Lambkin 2004). Following these releases, the impact of the parasitoid on whitefly populations on Thursday Island was monitored.

In this paper, the efficacy of *E. dispersa* in controlling *A. dispersus*, in terms of densities of whitefly nymphs per leaf area, and per cent parasitism and per cent infested leaves are documented in Australia for the first time on two common tropical ornamental plant species, *Terminalia catappa* L. (Combretaceae) (sea almond) and *Acalypha wilkesiana* Müll. Arg. (Euphorbiaceae) (beef steak). In addition, an appraisal of the ongoing impact of the parasitoid approximately a decade later is made. The suspected effects that the northern Australian monsoon season and plant structure have on the population dynamics of *A. dispersus* are discussed, and in addition, other insect predators of *A. dispersus* collected from Thursday Island are identified and recorded. Finally, we speculate on the likelihood that convoluted leaves of *A. wilkesiana* provide a host refuge, enabling effective ongoing biological control by *E. dispersa*.

Fig. 1. Top: mature specimen of *Acalypha wilkesiana* with flat leaves (Thursday Island), approximate height 3 m; and bottom: leaves infested with *Aleurodicus dispersus*.

MATERIALS AND METHODS

Just after the 1994 monsoon wet season, stocks of *E. dispersa* pupae within whitefly nymphs, free of plant material, were transported from Boigu Island in May and June and released immediately into whitefly colonies at 22 sites across Thursday Island (Lambkin 2004). Thursday Island has a tropical monsoon climate with a typical brief wet season predominately occurring between December and April. After parasitoid releases were made, 12 mature plants holding infestations of *A. dispersus* were monitored sporadically over 7 years to determine the impact of the parasitoid on whitefly populations.

All plants were within 150 m of where 100 parasitoids were released in May 1994 (Lambkin 2004). The host plants were six *A. wilkesiana* (beef steak), a variety with flat leaves (Fig. 1); four *A. wilkesiana*, a variety with convoluted leaves (Fig. 2); and two *Terminalia catappa* (sea almond) (Fig. 3). These plant types were chosen to monitor, as heavy whitefly infestations were observed on them (Lambkin 1999, 2004). Live and parasitised fourth-instar whitefly nymphs on 100 randomly sampled leaves of each plant were counted per sample date and from these data, mean whitefly densities/cm^2 of underside leaf area, percentage leaves infested and percentage whitefly parasitism were calculated for each plant type on each sample date. Monitoring commenced at the time of the parasitoid release in May 1994 and continued till April 1996. Due to the remoteness of the region, just nine monitoring visits were possible over this 2-year period, and a further two follow-up assessments were made later in June 1997 and March 2001, approximately 3 and 7 years after parasitoid releases (Lambkin 2004). Collected data were analysed using repeated measures ANOVA in GenStat 9 (2006). To stabilise the variance, arcsin (percentage data) and square root (density data) transformations were applied to the data before analysis. Comparisons between means were made using Fisher's protected Least Significant Difference (LSD) test. The variance ratios and LSDs for the time and interaction terms were adjusted for the degree of autocorrelation between times by the Greenhouse–Geiser epsilon (Greenhouse and Geiser 1959).

Fig. 2. Top: mature specimen of *Acalypha wilkesiana* with convoluted leaves (Thursday Island), approximate height 1 m; and bottom: leaves infested with *Aleurodicus dispersus*.

In addition, in February 2004, January 2006 and January 2008, return visits were made to two other islands in Torres Strait (Horn and Dauan), where large whitefly populations occurred before parasitoid release (Lambkin 2004), and visual appraisals of whitefly densities were made on the same host plant species as a measure of the ongoing long-term impact of the parasitoid on its host.

Determining densities of whitefly nymphs

One hundred mature leaves from each of the 12 infested plants (Figs 1–3) were randomly collected on each monitoring visit, examined under a microscope (Wild – portable stereo microscope, 6–50× magnification) and fourth-instar nymphs of *A. dispersus* counted using the method of Lambkin (2004). Because the leaves of each host plant varied considerably in size and shape, it was decided to compare whitefly densities within and between plant types on a per cm^2 leaf area basis, rather than per leaf. These densities were plotted against sample dates.

Fig. 3. Top: mature specimen of *Terminalia catappa* (Thursday Island), approximate height 4 m; and bottom: leaves infested with *Aleurodicus dispersus*.

Measurements of mean leaf areas for the three plant types were determined by randomly sampling mature leaves from mature plants and photocopying all leaves onto A4 sheets of paper (between 20 and 26 leaves of each plant type). Leaves that were too large to be photocopied singly were cut into two or three pieces and photocopied piecemeal. For each plant type, the photocopied images of all leaves were cut out and weighed. Because photocopied images of leaves were composed of a mixture of light and dark tones, the mean weights of photocopied leaves were compared with the mean combined weights of 10 white and 10 darkened photocopied squares of paper, each square 100 cm^2 in area. From these data, mean weights in g/cm^2 of grey-toned photocopied paper were calculated such that an estimated total leaf area for the 100 sampled leaves from each plant type and a mean surface area/leaf ($cm^2 \pm$ SE/leaf) could be made. Therefore average densities of nymphs/cm^2 of leaf area for each plant type were determined. Mean leaf surface areas calculated for the three plant types were ($cm^2 \pm$ SE): 187.4 ± 31.0 for *T. catappa*, 161.8 ± 32.2 for *A. wilkesiana* (flat) and 114.6 ± 15.5 for *A. wilkesiana* (convoluted).

Determining percentage 'infested leaves'

For this study, 'infested leaves' were designated as having at least one attached live whitefly nymph. Therefore, a mean percentage infested-leaf value for the three plant types at each sampling date was determined by dividing the number of 'infested leaves' by the total number of leaves (including 'infested') for each plant type. These percentage values were then plotted against sample date.

Measuring percentage parasitism

Parasitised fourth-instar whitefly nymphs were designated as nymphs that contained live parasitoid pupae or had recent parasitoid emergence. Nymphs with recent parasitoid emergence holes (generally less than 1 week since emergence) were those that were found to be clean of surface mould (Lambkin 2004). Total live and parasitised nymphs per plant type per sample date were counted using the method described by Lambkin (2004) and using these raw data converted to average percentage parasitism for each plant type. This entailed dividing the number of parasitised whitefly nymphs (including exuviae with fresh exit holes) by the total number of whitefly nymphs including parasitised (and then converting to percentage). Average percentage parasitism values were plotted against sample dates and were also plotted against whitefly densities at the start and end of the study.

Relating whitefly density and percentage parasitism

Overall declines in whitefly densities from pre-introduction density (K) to post-introduction densities (N^*), expressed as a ratio (q), were compared with the work of Beddington *et al.* (1978) to test for 'successful classic' biological control with parasitoids, in particular those that normally rely on a refuge (Murdoch *et al.* 1985). In addition, when treating percentage parasitism as an estimate of parasitoid population size, percentage parasitism and host density data were plotted as a phase plane (Murdoch *et al.* 1985) to test each plant type for stable whitefly–parasitoid equilibriums (likely based on refuges). To further show stable equilibriums linked to refuges, we used a host–refuge model, as in Beddington *et al.* (1978), in which the host, H_t, and parasitoid population, P_t, were modelled as a pair of standard difference equations for host–parasitoid interactions:

$$H_{t+1} = H_t\phi \mathrm{e}^{r(1-Ht\phi/K1)}\mathrm{e}^{-a1Pt} + H_t(1-\phi)\mathrm{e}^{r(1-Ht(1-\phi)/K2)}\mathrm{e}^{-a2Pt}$$

$$P_{t+1} = c\left(H_t\phi(1-\mathrm{e}^{-a1Pt}) + H_t(1-\phi)(1-\mathrm{e}^{-a2Pt})\right)$$

where ϕ is the proportion of the population in a refuge, $K1$ and $K2$ are the carrying capacity of the whitefly outside and inside the refuge, $a1$ and $a2$ were the respective search efficiencies of the parasitoids, r is the host's innate capacity to increase and c is the proportion of parasitised hosts that survive to give rise to new parasitoids. To generate such an effect, we set the population growth rate for *A. dispersus* at 1.17 (=$\mathrm{e}^{0.16}$) (estimate based on Wen *et al.* 1994b, 1996) and a 10% refuge (i.e. $\phi = 0.1$), in which search efficiency '$a1$' was low (0.01) (for exposed populations, i.e. $1 - \phi$, parasitoids have a much higher search efficiency, '$a2$' = 0.3). Finally for our simulation we set $K1 = K2 = 3000$ and c to 0.2 (Beddington *et al.* 1978).

Identifying other insect predators of *A. dispersus*

Over the monitoring period, other insect predators that were observed feeding on live nymphs of *A. dispersus* were collected from Thursday Island, killed and transported to Brisbane for mounting and identification. Specimens of *Cryptolaemus affinis* and *E. dispersa* were deposited in the Primary Industries and Fisheries Collection; Department of Employment, Economic Development and Innovation – Brisbane, Australia, and *Acletoxenus quadristriatus* in the Australian Museum – Sydney, Australia.

RESULTS

Densities of whitefly nymphs

Analysis of whitefly density data gave a significant interaction ($P = 0.014$) indicating differing response patterns for the densities on each plant type over time (Fig. 4). Maximum whitefly densities on all plants were recorded over the first three sample dates up until and including October 1994. Over this period, whitefly numbers were relatively stable, with the highest mean density of 0.34 whitefly nymphs/cm^2 recorded on *T. catappa* at the first sample date in May 1994. On the two types of

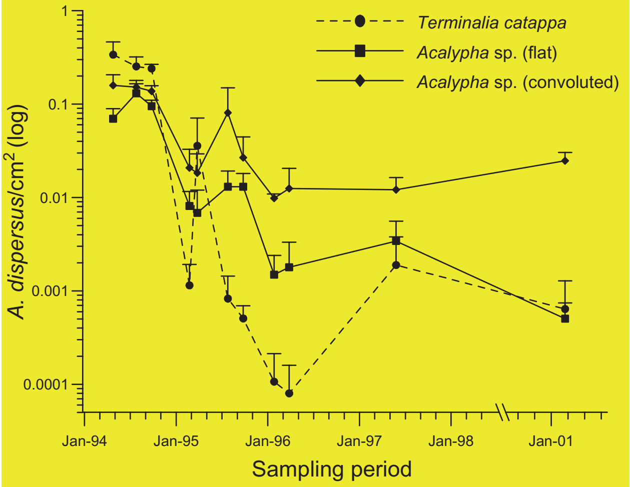

Fig. 4. Mean log densities of fourth-instar nymphs (± SE) of *Aleurodicus dispersus*/cm^2 leaf area on *Terminalia catappa* and *Acalypha wilkesiana* (with flat and convoluted leaves) recorded on Thursday Island at 11 sample dates, May 1994–March 2001; parasitoids were released May 1994. Average Least Significant Difference (LSD) (5%) = 0.15 except for comparisons within a plant type when average LSD (5%) = 0.13. Comparisons should be made on the square root transformed data.

A. wilkesiana, average densities of whitefly nymphs at the first sample date were significantly lower than on *T. catappa*, but were not significantly different from each other. Afterwards, between the time of the third (October 1994) and fourth sample date (March 1995), approximately 10 months after the parasitoid release, all whitefly densities declined significantly. This latter period also coincided with the onset of the wet season in Torres Strait. In all cases, whitefly densities resurged in 1995 to various degrees, but at no time to the same levels that were recorded earlier (Fig. 4). Later assessments of whitefly densities made in June 1997 and March 2001 indicated that whitefly densities, approximately 37 and 82 months after parasitoid releases, were still significantly lower than densities recorded before establishment of the parasitoid (Fig. 4). The greatest decline was observed on *T. catappa*, with whitefly density dropping to approximately 0.001 whitefly nymphs/cm^2 after 82 months, i.e. approximately 0.2% of the original value before parasitoid release. Although whitefly density was initially significantly higher on *T. catappa*, by late 1995 the density had dropped to below the levels of the other two plant types and remained mostly lower from then on. At this same time, whitefly density on the flat-leafed variety of *A. wilkesiana* was also low at approximately 0.7% of the original value before parasitoid release (Fig. 4). On the convoluted-leafed variety of *A. wilkesiana* however, density remained higher (0.025 whitefly nymphs/cm^2), at around 15% of the original value.

Visual appraisals of whitefly densities on the three plant types made at the start of the wet seasons in 2004, 2006 and 2008 on Horn and Dauan (two other Torres Strait islands previously with high whitefly numbers) indicated that *A. dispersus* still remained suppressed 10–12 years after the release of *E. dispersa* into Torres Strait. As for the earlier assessments, the convoluted-leafed variety of *A. wilkesiana* had relatively larger numbers of whiteflies than the other two plant types, albeit all in comparatively lower densities than years earlier.

Percentage infested leaves

Analysis of these data gave a significant interaction ($P = 0.027$) indicating differing response patterns for percentages of infested leaves for each plant type over time (Fig. 5). The data roughly followed the same trend as the density of *A. dispersus* over the same period. At the start of the study, average percentages were between 63 and 88, and these dropped dramatically over the time of the first wet season (December–April 1995) in keeping with the general drop in whiteflies and the rise in parasitoid numbers. Following this time, almost all values of percentage infested leaves remained low (<15%), and fell progressively, except for *A. wilkesiana* with convoluted leaves, whose average value increased to 36% during the 1995 dry season (August) and was still around 10% in March 1996 compared with 2.3% for *A. wilkesiana* with flat leaves and 0.5% for *T. catappa* (Fig. 5). Similar values of percentage infested leaves were observed, respectively, on each plant type approximately 37 and 82 months after parasitoid release. At these times, values were significantly lower for *A. wilkesiana* with flat leaves (7% and 2%, respectively) and for *T. catappa* (5% and 3.5%, respectively) with significantly higher values persisting on *A. wilkesiana* with convoluted leaves (15% and 21.5%, respectively).

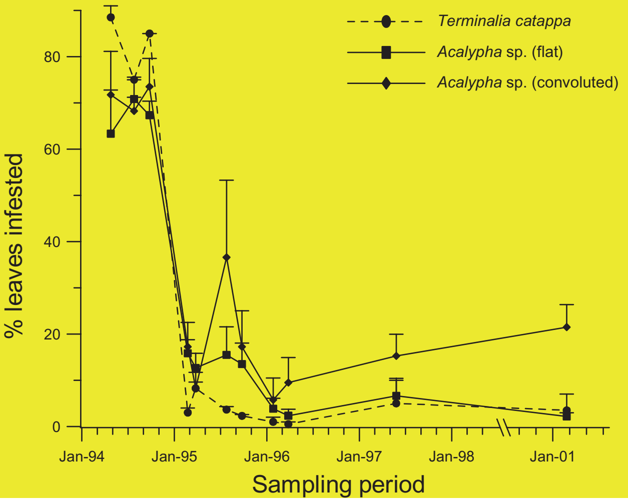

Fig. 5. Mean percentage leaves infested (± SE) with *Aleurodicus dispersus* for *Terminalia catappa*, and *Acalypha wilkesiana* with convoluted and flat leaves recorded on Thursday Island at 11 sample dates, May 1994–March 2001 (infested leaves were designated by having at least one attached live whitefly nymph); parasitoids released May 1994. Average Least Significant Difference (LSD) (5%) = 0.14 except for comparisons within a plant type when average LSD (5%) = 0.11. Comparisons should be made on the arcsin transformed data.

Percentage parasitism

Analysis of parasitism indicated no significant difference in the response between each plant host (type) over time ($P = 0.250$); however, there were significant plant type effects ($P = 0.046$) with parasitism rates on *T. catappa* (10.4%) significantly greater than both leaf types of *A. wilkesiana* (3.8% convoluted and 4.6% flat) (average LSD (5%) = 0.100 on transformed data, Fig. 6). In addition, for all plant types, there were significant differences in rates of parasitism over time ($P < 0.001$) with significant peaks in March/April 1995 and again in March 2001 (LSD (5%) = 0.241 on transformed data, Fig. 6). In general, for all declines in whitefly numbers observed over the first 2 years of monitoring, a corresponding increase in percentage parasitism occurred on all hosts, with the highest increase of almost 80% recorded on *T. catappa* in March 1995. From late 1995 to early 1996 parasitism rates increased again on *T. catappa* and on *A. wilkesiana* with flat leaves, roughly corresponding with declines in whitefly densities. The exception to this was a resurgence of whitefly density on convoluted leaves of *A. wilkesiana* during the dry season of 1995 (Fig. 4) without a corresponding increase in parasitism (Fig. 6). Relatively high whitefly densities with low parasitism rates were also recorded on convoluted leaves of *A. wilkesiana* in March 2001 (Figs 4,6). Twelve months after parasitoid releases had been made (March 1995), whitefly

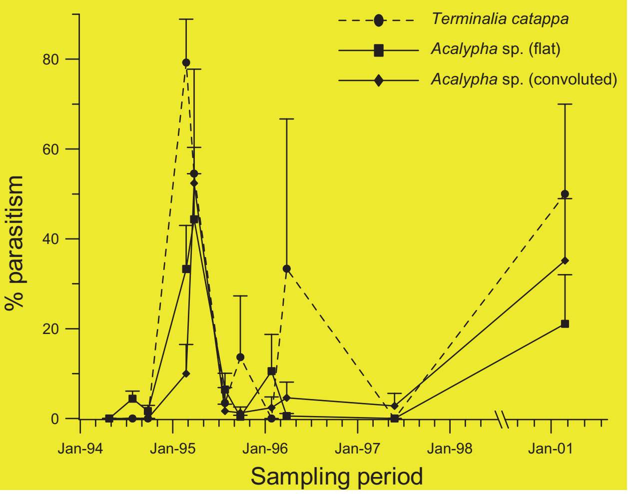

Fig. 6. Mean parasitism (percentage) of fourth-instar nymphs (± SE) of *Aleurodicus dispersus* by *Encarsia dispersa*: recorded on Thursday Island on three hosts (*Terminalia catappa*, and *Acalypha wilkesiana* with flat and convoluted leaves) at 11 sample dates, May 1994–March 2001; parasitoids were released May 1994.

densities were generally low except on *A. wilkesiana* with convoluted leaves, which had highly variable percentage parasitism (Fig. 7a). In March 2001, percentage parasitism was still variable with whitefly densities mostly low, except on *A. wilkesiana* with convoluted leaves (Fig. 7b).

Relating whitefly density and percentage parasitism

The overall whitefly density decline on each plant type, defined as the ratio (q), was of the order of magnitude, i.e. *c.* 0.01 (Beddington *et al.* 1978), expected for successful classic biological control programs with parasitoids. Murdoch *et al.* (1985) indicated that such declines theoretically are usually achieved in models that contain a refuge. The phase plane curves showed the plot spiralling inwards for *A. wilkesiana* with convoluted leaves suggesting a stable equilibrium for this host but not so for the other hosts (Fig. 8). Given the degree-day requirements for the host (*c.* 430 DD above 5°C) (Wen *et al.* 1994b, 1996) we estimated *c.* 21 whitefly generations/year in Torres Strait with the final equilibrium density of the whitefly host about 3–7% of the initial density. In addition, using the host–refuge model of Beddington *et al.* (1978) with our parameters, host populations declined steeply, then rebounded with damped oscillations with noticeable increases after 30–45 (1.5–2 years) and 70–80 generations (3.5–4 years).

Other insect predators of *A. dispersus*

Apart from *E. dispersa*, adults and larvae of *Cryptolaemus affinis* Crotch (Coleoptera: Coccinellidae) and larvae of *A. quadristriatus* Duda (Diptera: Drosophilidae) were the only other insects causing mortality of *A. dispersus* nymphs on Thursday Island over the period of the study. During the first half of the study, when large numbers of whitefly nymphs were present on each plant at each sample date, both of the above species were encountered frequently.

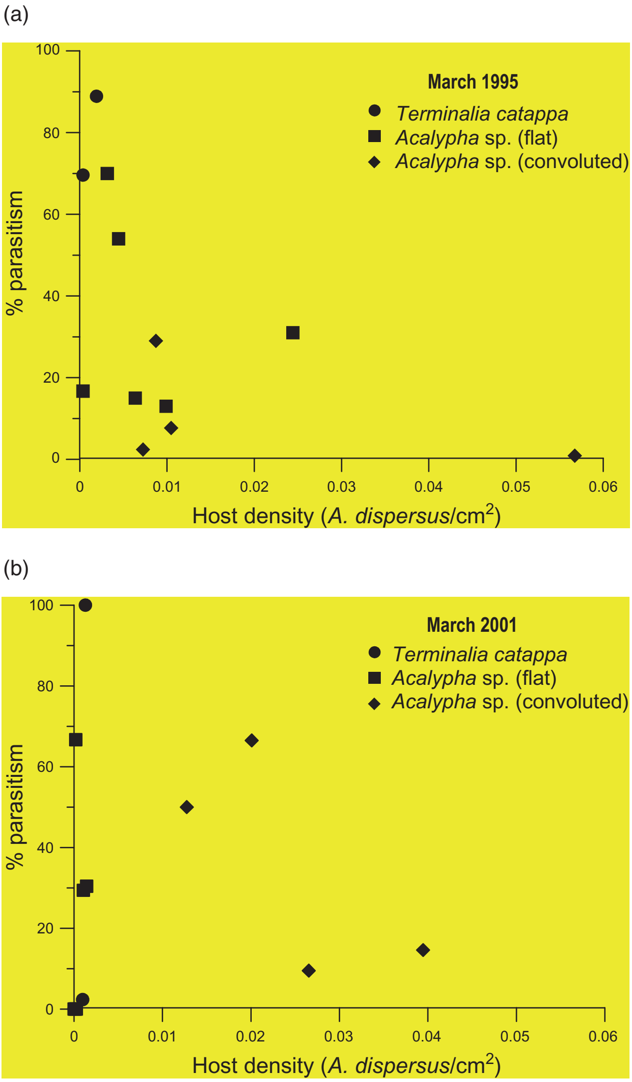

Fig. 7. Percentage parasitism vs. density of *Aleurodicus dispersus* on each of three plant types: (a) early in the biological control period (March 1995), and (b) well after the parasitoid had become established (March 2001).

DISCUSSION

Attempts to establish *E. dispersa* for the biological control of *A. dispersus* and to measure its subsequent impact have been reported in Hawaii (Kumashiro *et al.* 1983), Pohnpei in the Federated States of Micronesia (Esguerra 1989), Benin (Neuenschwander 1996; D'Almeida *et al.* 1998) and Taiwan (Chien *et al.* 2000). Oddly enough, Chien *et al.* (2000) could not establish the parasitoid in Taiwan despite releasing around 57 000 adults of *E. dispersa* over a 2-year period. Apart from Chien *et al.* (2000), when using *E. dispersa*, marked declines

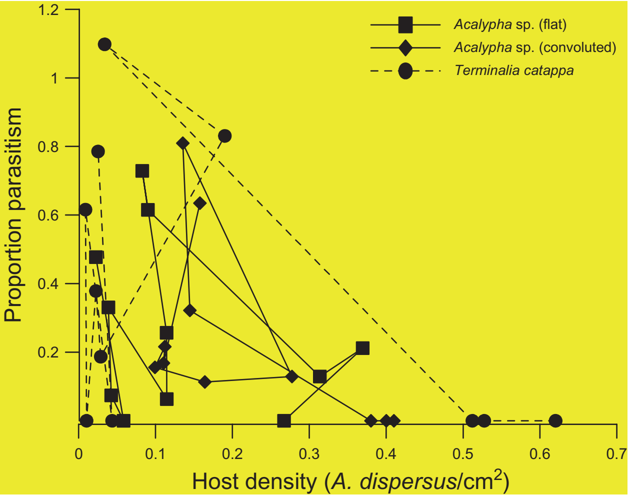

Fig. 8. Phase plane plot of proportion (derived from percentage) parasitism by *Encarsia dispersa* vs. *Aleurodicus dispersus* density/cm^2 on each of three plant types; axes have been arcsin square root transformed to display the data better.

in whitefly numbers have been recorded by all other workers approximately 1–3 months after the first recovery of the parasitoid. This was similar to the Thursday Island study where significant declines in whiteflies were recorded between 2 and 6 months after first detection of the parasitoid (Lambkin 2004). In 1995 and 2001, apart from *A. wilkesiana* with convoluted leaves, overall percentage parasitism was inversely related to whitefly density (Fig. 7). Such inverse density dependence has been found in other successful biological control programs (Walde & Murdoch 1988).

Over the time of the study, densities of *A. dispersus* quickly fell to very low levels except on *A. wilkesiana* with convoluted leaves. Approximately 7 years after the release of *E. dispersa*, whitefly densities on *A. wilkesiana* with flat leaves and on *T. catappa* were less than 1% of the original values recorded at the time of the parasitoid release, but on *A. wilkesiana* with convoluted leaves, the whitefly density was still about 15% of the original value. This same trend occurred for percentage infested leaves recorded over the 7-year period. D'Almeida *et al.* (1998) in West Africa found that proportions of infested leaves/host plant were strongly dependant on whitefly densities and that, as in the Thursday Island study except on *A. wilkesiana* with convoluted leaves, proportions of infested leaves that they measured declined significantly with the duration of the presence of the parasitoid.

Kumashiro *et al.* (1983) monitored the impact of *E. dispersa* on *A. dispersus* in two climatic zones in Hawaii and found that numbers of whiteflies in lowland Honolulu (which is much drier than highland Honolulu) rebounded markedly during the first dry season after parasitoid establishment as opposed to a much smaller rebound over the same period in the wetter highland areas. D'Almeida *et al.* (1998) also found that, in general, dry conditions favoured proliferation of whiteflies. They suggested that lower whitefly numbers recorded during wet seasons were attributed to a 'washing-off effect' of the whiteflies by rain, combined with an improved physiological condition of the host plant over these wetter months. Conversely, in the dry, there are less physical disturbances of the whiteflies including a greater stress placed on host plants because of the protracted dry season, which when combined, might allow whitefly numbers to increase. In contrast, Esguerra (1989) on Pohnpei, who monitored parasitism of *A. dispersus* on *A. wilkesiana*, did not note any declines in whiteflies over the island's wet season. On Thursday Island, after parasitoid establishment was detected, particularly steep declines in whitefly densities were recorded during the wet seasons on the two hosts that had a more open leaf structure (*A. wilkesiana* with flat leaves and *T. catappa*) (Fig. 4). On these hosts, whiteflies may have been more susceptible to the effects of falling rain than whiteflies on *A. wilkesiana* with convoluted leaves as D'Almeida *et al.* (1998) reported.

The much higher overall values of percentage infested leaves recorded in the latter part of the study for *A. wilkesiana* with convoluted leaves additionally indicate that whiteflies were more difficult to control on this host (Fig. 5). This seemed to be related to the convoluted leaf structure of the *Acalypha* (Fig. 2). This particular leaf structure likely provides physical refuges for whitefly nymphs thereby inhibiting parasitism by *E. dispersa* (Fig. 6). In contrast, whitefly densities on *T. catappa*, which has very flat leaves with an open growth structure, started significantly higher than on both *Acalypha* types but after parasitoid releases were made, whitefly densities dropped to the lowest levels recorded, and remained low from then on (Fig. 4). Besides the convoluted leaves of *A. wilkesiana* providing possible refuges for whitefly nymphs to avoid parasitism, they might also inhibit the 'washing-off effect' of rain, particularly during wet seasons, thereby providing higher whitefly densities and more infested leaves at the start of subsequent dry seasons.

It was unclear if the presence of the native predators, *C. affinis* and *A. quadristriatus*, had an impact on whitefly densities on Thursday Island. Mani and Krishnamoorthy (2000) recorded 13 native predators of *A. dispersus* in India including *Cryptolaemus montrouzieri* Mulsant and *Acletoxenus indicus* Malloch, but they could detect no discernable impact of the predators on whitefly numbers. However, in Hawaii, Kumashiro *et al.* (1983) tested the potential of *Nephaspis amnicola* Wingo (Coccinellidae) in controlling *A. dispersus* and found that the coccinellid contributed markedly to reducing whitefly numbers but did so only when whitefly nymphs were at high densities. This may have been the case on Thursday Island as each of the two predators was most frequently observed when whitefly densities were high, mostly at the start of the study, or in the case of *A. wilkesiana* with convoluted leaves, at any time over the study period.

Our model analysis suggests that whitefly resurgence on convoluted *A. wilkesiana* on Thursday Island might also be a function of host parasitoid interactions and not just a result of seasonal effects. These ongoing interactions could be driven by refuges occurring within specimens of *A. wilkesiana* with convoluted leaves. Removing these refuge plants with convoluted leaves could generate unstable host parasitoid dynamics, which may result in the host resurging with parasitoid extinction, or extinction of the parasitoid and the host. There are insufficient sampling data to currently test this hypothesis but the system in Torres Strait might be ideal for future experimental studies.

In summary, the data presented here agree with the results of previous workers in that control of *A. dispersus*, at least in the short term, seems possible with an inoculative release of the parasitoid, *E. dispersa*. Despite the parasitoid being highly effective in the long term, some hosts such as *A. wilkesiana* with convoluted leaves might offer protected environments or physical refuges that inhibit the efficacy of the parasitoid, particularly in dry weather, but could inversely maintain the stability of the biological control. This is important to remember when making parasitoid releases and monitoring subsequent control, particularly on horticultural species with closed leaf structures, and especially in irrigated areas of the dry tropics that experience relatively long periods of warm weather without precipitation. Finally, considering the pest's wide host range and the propensity for twisted leaf structures of some plant species to harbour relatively large numbers of *A. dispersus*, movements of infested plants or parts of plants within or out of tropical Australia, in particular varieties of *A. wilkesiana*, pose a significant quarantine risk.

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