Biological control of *Bemisia argentifolii* (Hemiptera: Aleyrodidae) on poinsettia with inundative releases of *Eretmocerus eremicus* (Hymenoptera: Aphelinidae): do release rates affect parasitism?

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Abstract

The effectiveness of inundative releases of the parasitoid *Eretmocerus eremicus* n. sp. Rose & Zolnerowich for control of *Bemisia argentifolii* Bellows & Perring on poinsettia in replicated experimental greenhouses was determined. We evaluated two release rates of *E. eremicus:* a low release rate (one female per plant per week, released in two greenhouses, in spring 1995) and a high release rate (three females per plant per week, released in two greenhouses, in spring 1994), each over a 14 week growing season. Each release trial had either one (1995) or two (1994) control greenhouses in which *B. argentifolii* developed on poinsettia in the absence of *E. eremicus*. Life-tables were constructed for *B. argentifolii* in the presence and absence of *E. eremicus* by using a photographic technique to follow cohorts of whiteflies on poinsettia leaves. Weekly population counts of whiteflies were also made. In the absence of *E. eremicus,* egg to adult survivorship of *B. argentifolii* on poinsettia was 75–81%. At the low release rate, egg to adult survivorship of *B. argentifolii* was 12% and parasitism was 34%. At the high release rate, egg to adult survivorship of *B. argentifolii* was 0.9% and parasitism was 10%. The average net reproductive rates (R_o) for populations of *B. argentifolii* in the absence of *E. eremicus* ranged from 20.5 to 26.1, indicating a rapidly increasing population density. Net reproductive rates for whitefly populations subject to parasitoid releases were 3.7 in the low release rate greenhouses, and 0.25 in the high release rate greenhouses, indicating substantially reduced *B. argentifolii* population growth. At week 14 of the trial, densities of immature whiteflies were lower in greenhouses at the low release rate when compared to the high release rate greenhouses. This was attributed to high levels of in-house reproduction by parasitoids at the low release rate.

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Introduction

The major whitefly pest of poinsettia, *Euphorbia pulcherrima*, in northeastern United States greenhouses is the silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring (Hemiptera: Aleyrodidae) [=the 'B' strain of *B. tabaci* (Gennadius) (Bellows *et al*., 1994)]. This whitefly became problematic on poinsettia in Massachusetts in 1987, following its probable introduction and distribution from Florida in 1986 (Hoddle *et al*., 1996a). Prior to the registering of imidacloprid (a systemic chloronicotinyl insecticide which gives 10–12 weeks whitefly control with a single application) in Massachusetts in 1994 (Lopes, 1994), this whitefly was controlled with foliar insecticide applications which were often applied on a 3–5 day calendar schedule (Hoddle & Van Driesche, 1996). Development of resistance to imidacloprid by *B. argentifolii* is expected because this whitefly has developed resistance to this compound on outdoor vegetable crops in Spain (Cahill *et al*., 1996).

As part of an integrated pest management (IPM) project to reduce resistance development and improve *B. argentifolii* management on poinsettia in Massachusetts, we have been evaluating the ability of natural enemies (hymenopterous parasitoids) for the biological control of *B. argentifolii* (Hoddle *et al*., 1997).

One natural enemy that has been considered for use in the IPM programme is *Eretmocerus eremicus* n. sp. Rose & Zolnerowich (Hymenoptera: Aphelinidae) (Rose & Zolnerowich, 1997). *Eretmocerus eremicus* is a bi-parental parasitoid (in culture this parasitoid has a 1:1 sex ratio [Minkenberg, unpublished]) native to the southwest USA that is currently being mass reared and marketed for whitefly control. Species of *Eretmocerus* dominate the parasitoid fauna found attacking *B. argentifolii* on outdoor crops in the southwest USA (Hunter *et al*., 1996; Rose & Zolnerowich, 1997), and members of this genus develop as primary ecto-endoparasitoids of whiteflies (Rose & Rosen, 1991–1992; Gerling, 1986; Gerling *et al*., 1990, 1991). Female parasitoids oviposit under suitable hosts, and parasitoid larvae, after hatching, penetrate the ventral surface of hosts, and develop as solitary endoparasitoids (Gerling, 1966, 1986; Gerling *et al*., 1990, 1991). *Eretmocerus eremicus* will feed on haemolymph after engaging the ovipositor in the vasiform orifice of the host (Headrick *et al*., 1995). Killing hosts in this manner for nutritional purposes is termed host feeding. Species of *Eretmocerus* have been used in successful classical biological programmes for whiteflies, e.g. *Eretmocerus serius* Silvestri for control of citrus blackfly, *Aleurocanthus woglumi* Ashby (Hemiptera: Aleyrodidae) and *Eretmocerus debachi* Rose & Rosen for control of bayberry whitefly, *Parabemisia myricae* (Kuwana) (Hemiptera: Aleyrodidae) (Rose & Rosen, 1991–1992).

Augmentative releases of mass-reared *E. eremicus* have been assessed for control of *B. argentifolii* on cotton in southern California (Minkenberg *et al*., 1994; Simmons & Minkenberg 1994). Evaluations of inundative releases of *E. eremicus* for *B. argentifolii* control on ornamentals, in particular, greenhouse-grown poinsettias, have not been made.

Our objectives were to use paired life-tables and population counts to determine over the course of a 14 week poinsettia crop: (i) the suppressive effect of *E. eremicus* on *B. argentifolii* population growth when compared to whitefly population growth in the absence of this natural enemy; (ii) whether our low and high release rates of *E. eremicus* differed in the level of control provided; and (iii) what mechanisms governed the effects of these parasitoid releases on whitefly population growth.

Materials and methods

Experimental greenhouses, crop management, and initial whitefly infestation levels

Evaluations of *E. eremicus* were conducted in small identical plastic greenhouses at Cornell University, Ithaca, New York. Each greenhouse (5×4×3.5 m) held six benches (0.91×1.5×0.91 m) each with 15 pots (15 cm diameter, with single stem poinsettias) for a total of 90 plants per greenhouse. The spring trial in 1994 included two control greenhouses (no parasitoids released) and two parasitoid release greenhouses (three females per plant per week). The spring trial in 1995 included three greenhouses: one control greenhouse and two parasitoid release greenhouses (one female per plant per week). Four dichlorvos fumigant strips were hung in each control greenhouse to exclude invading parasitoids. This slow release formulation excluded parasitoids from our *B. argentifolii* colony with no apparent effect on whitefly survivorship. The poinsettia cultivar used for the spring trial in 1994 (high release rate) was 'Celebrate II' and for the spring trial in 1995 (low release rate) 'Freedom Red' was used. The two poinsettia cultivars did not differ in leaf trichome densities (Sanderson, unpublished), a factor that can affect parasitoid efficacy on poinsettia (Heinz & Parrella, 1994). Each trial ran for 14 weeks.

The 1994 and 1995 poinsettia crops were each started from rooted cuttings received from Paul Ecke Ranch, Encinitas, California, which had been grown without any use of systemic insecticides. After potting, plants were subjected to commercial management practices of fertilizer application (Peter's Exel® [15-5-5] at 200 ppm, Peter's Stem® at 0.11 g/litre, and MolyB® liquid concentrate at 0.18 ml/litre at every watering), root rot control (Subdue® [metalaxyl] applied at weeks 2 and 11 of each trial as a hand poured drench at a rate of 0.15 g/litre), and pinching (three weeks after potting). Maximum and minimum temperatures were recorded daily.

To determine if initial *B. argentifolii* densities on poinsettia cuttings differed between trials, we recorded the number of nymphs and adults on each leaf of 102 randomly chosen cuttings for each trial prior to potting.

Parasitoid release regimen

Two release rates of *E. eremicus* were evaluated. The high release rate consisted of weekly releases of three females per plant, and the trial was conducted in spring 1994 (March 22 to July 27, 1994 inclusive). The low release rate was one female per plant per week and the test was run in spring 1995 (February 17 to May 25, 1995 inclusive). *Eretmocerus eremicus* was mass-reared at the University of Arizona, Tucson, and shipped as loose parasitized *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) nymphs. Voucher specimens of *E. eremicus* were lodged with the Entomology Museum, University of California at Riverside. After receipt,

parasitized nymphs were divided amongst petri dishes with honey streaked on lids (as a food supplement) and parasitoids were allowed to emerge. Prior to release, the number of females was counted in petri dishes using a dissecting microscope in the laboratory. Petri dishes with parasitoids (males and females) were then taken to greenhouses, evenly distributed under the plant canopy and opened. Parasitoids were released in this manner until the desired weekly release total of females had been achieved for each greenhouse.

Establishing and photographing whitefly cohorts, constructing life-tables and survivorship curves

The fates of cohorts of whitefly nymphs (1–87 whitefly nymphs per patch) on poinsettia leaves were determined using a photographic technique, and the resultant photographic slides were used to construct life-tables for *B. argentifolii* in the presence and absence of *E. eremicus* (after Summy *et al.*, 1984; Gould *et al*., 1992; Hoddle *et al*., 1996b).

To establish a cohort of whiteflies, 10–13 poinsettia plants from each greenhouse were taken to the laboratory and clip cages were placed on one leaf of each plant. In each cage, one to four mating pairs of whiteflies were introduced and left to oviposit for 2–3 days at 25°C. Cages and whiteflies were then removed, the number of eggs laid recorded, and plants placed in their respective greenhouses. By varying the number of adult whiteflies in clip cages we produced whitefly patches of different densities. Whitefly patches on individual poinsettia leaves are referred to as sub-cohorts. Contemporary sub-cohorts within a greenhouse are collectively referred to as cohorts.

Egg numbers on artificially infested leaves were standardized by removing eggs from sub-cohorts with a 000 size insect pin so that similar egg totals were added to each greenhouse each time cohorts were established. Sub-cohorts were set up for photography at weeks 1 and 2 (designated whitefly cohorts 1 + 2), 5 (cohort 3) and 9 (cohort 4) of the trial. These cohorts correspond to the first, second, and third generations of whiteflies. Eight to ten days after whiteflies were removed from clip cages, the numbers of first instars that had emerged and settled from the counted eggs were recorded. A 35 × 23 mm area of leaf on which most nymphs had settled was photographed. Photography commenced immediately after nymphs in each sub-cohort had settled on leaves. Each sub-cohort was photographed twice on each sample date (an insurance measure against unfocused slides), and photography was repeated twice each week. Photography of sub-cohorts ceased when either all the nymphs had died, disappeared, emerged as adult whiteflies, or produced adult parasitoids.

The camera used was a 35 mm SLR fitted with a 55 mm macrolens, a dedicated ringflash, and one extension tube. F-stop and aperture settings were at 16 and 22, respectively. Colour slide film (50 ASA) was used.

Slides of each sub-cohort were analysed in chronological order using a back-lit dissecting microscope at 10× magnification. The fates of individual whitefly nymphs were recorded on leaf maps, with a distinct leaf map being drawn for each photographic date. The number of eggs required to produce the number of settled first instars that were observed in the first photograph of each cohort was calculated by dividing the number of photographed nymphs by the proportion of nymphs that settled on the leaf from the original egg mass (see Hoddle *et al*. (1996b) for more details on the photography method).

The number of nymphs entering each instar, the number disappearing and dying in each instar, and the causes of all mortality were recorded and used to construct life-tables. Data from sub-cohorts were combined to produce life-tables for each whitefly cohort in each treatment. Life-tables were combined across replicates. Summary life-tables were developed by combining cohorts within treatments.

Survivorship curves for *B. argentifolii* were constructed from summary life-table data for each treatment. Percent survival for each developmental stage was calculated as the number of nymphs that lived to enter stage *i*, divided by the initial number of eggs used to establish the photographed nymphs.

Calculating marginal probabilities of mortality

To separate mortality from each observed source (unknown death, disappearance, and parasitism) marginal mortality rates were calculated. The marginal probability of mortality is the number of whiteflies that would be attacked by an agent in the absence of all other contemporaneous mortality agents (Royama, 1981; Bellows *et al*., 1992; Elkinton *et al*., 1992). Since disappearance of whitefly nymphs was directly observable, marginal probability of disappearance was the same as the observed death rate. When disappearance and unknown death of nymphs in the same stage occurred concurrently, marginal probability of death from unknown causes (m_{ud}) was calculated from observed mortality as:

$$m_{ud} = d_{ud} / (1 - m_D) \quad [1]$$

where d_{ud} is Death from Unknown Causes observed with photographic sampling, and m_D is the marginal rate of Disappearance (=observed death rate) (Elkinton *et al*., 1992; Gould *et al*., 1992).

The marginal probabilities of mortality for three contemporaneous factors were calculated as:

$$m_i = 1 - (1 - d)^{d_i / d} \quad [2]$$

where m_i is the marginal probability of mortality from the *i*th cause, d_i is death rate from the *i*th cause, and d is death rate from all causes combined (Elkinton *et al*., 1992).

Sex ratio of emerging whiteflies, net fecundity estimates, and calculation of net reproductive rates (R_o)

Sex ratio [females / (males + females)] for *B. argentifolii* on poinsettia is positively correlated with temperature. The relationship between sex ratio and temperature for the temperature range 19–28°C is described by the equation $SR = 0.02T + 0.25$, $r^2 = 0.97$, where SR is sex ratio and T is temperature (Enkegaard, 1993). The average temperature ([daily maximum + minimum temperatures] / 2) experienced by each photographed whitefly cohort over the course of its development was substituted into the above equation to estimate the sex ratio of the whiteflies which emerged from cohorts.

Enkegaard (1992) provided net fecundity (L_xM_x) estimates (where L_x is the fraction of females that survive to age x, and M_x is the gross fecundity at age x [Carey, 1993]) for *B. argentifolii* reared on poinsettia at five controlled temperatures (16–28°C). Net fecundity is positively correlated with

temperature, and is described by $NF = 6.3T - 102.1$, $r^2 = 0.97$, where NF is net fecundity and T is temperature (Enkegaard, 1992). The average temperature experienced by each photographed whitefly cohort over the course of its development was substituted into the above equation to estimate likely net fecundity for individual females emerging from cohorts.

Net reproductive rate (R_o) is the average number of female offspring born to a cohort of females during their lifetime, and describes the per cohort growth rate of the population (Carey, 1993). Sex ratio and net fecundity estimates were calculated as described above, and R_o was calculated by dividing the theoretical fecundity of females emerging from photographed cohorts by the number of eggs used to establish those cohorts. Values of $R_o < 1$ indicate a declining population, $R_o > 1$ an increasing population, and $R_o = 1$ a stable population (Carey, 1993).

Monitoring B. argentifolii *population densities*

Population counts of immature and adult whiteflies on poinsettia leaves were made weekly. Numbers of first/second, third, fourth instars, pupae, exuviae from which either adult whiteflies or parasitoids had emerged, and adult whiteflies were recorded.

Over the course of the trial, plants were divided by height into three strata, and all immature whiteflies were counted on a fixed number of tagged leaves within each stratum. Stratum one consisted of the leaves originally present on the newly potted cuttings. For stratum one, one leaf on each of 15 randomly selected plants was tagged in each greenhouse and inspected weekly. After 5–6 weeks of plant growth, one leaf in the top portion of an additional 15 randomly selected plants was tagged in each greenhouse. These leaves were designated stratum two, and whitefly counts were made in both stratum one and two each week thereafter. After an additional 4–5 weeks of growth (around week 10–11 of the trial), another 15 plants in each greenhouse had one leaf tagged at the top of the plant and inspected weekly. This uppermost leaf layer was designated stratum three. At this time, 15 leaves were being examined weekly in each of three strata for a total of 45 leaves, one leaf on each of 45 plants in each greenhouse.

Each time a new stratum was established, the total number of leaves in that stratum was recorded for 10 plants in each greenhouse. Leaf counts within plant strata were used to determine the mean number of whiteflies (by life stage) per plant for each treatment.

Estimating parasitoid reproduction in greenhouses

The number of parasitoids emerging each week into the greenhouse via in-house reproduction was calculated from weekly estimated densities of nymphal exuviae from which parasitoids had emerged. Estimates of the number of newly emerged parasitoids per plant for each week of the trial were multiplied by the number of plants in the greenhouse to estimate the number of newly emerging parasitoids for the greenhouse as a whole. Since whitefly pupae from which parasitoids had emerged accumulated on leaves, each weekly estimate had the count from the preceding week subtracted from it to give net estimates of parasitoids emerging into the greenhouse. Weekly net estimates were then divided by two to approximate the numbers of females emerging into the greenhouses.

Estimating the number of hosts available per plant for parasitoid attack

Eretmocerus eremicus will parasitize first, second, third, and fourth instars (Headrick *et al*., 1995), and host feed on all immature lifestages, although this may be affected by the host plant (Headrick *et al.*, 1995, 1996). Whitefly pupae are immune to attack by species of *Eretmocerus* (Gerling, 1966). The number of susceptible hosts per plant available for attack by females averaged for each treatment, for each week of the trial, was calculated by adding the per plant densities of all whitefly stages suitable for parasitoid attack. The host:parasitoid ratio was then calculated by dividing the weekly estimate of susceptible stages by the estimated number of females per plant in the greenhouse. To estimate the population of parasitoids present in each greenhouse in specific weeks, the number of females released each week was added to the estimated number of females emerging from in-house parasitoid reproduction. Our estimates were calculated with the assumption that females survived in greenhouses for one week only. Survivorship of around 7 days has been recorded for *Eretmocerus* sp. when *B. argentifolii* is the host (McAuslane & Nguyen, 1996).

Estimating percent mortality and percent parasitism in experimental greenhouses

Average percent mortality (i.e. no. dead nymphs and pupae/[(no. dead nymphs and pupae) + no. live nymphs and pupae]) from causes other than successful parasitism (i.e. host feeding and aborted parasitism) and parasitism (i.e. no. parasitized nymphs/[no. parasitized nymphs + no. unparasitized nymphs]) estimates per plant per week for each parasitoid release treatment were calculated from the weekly *B. argentifolii* population counts.

End of crop sales inspection

At week 14 of the trial, 15 randomly selected plants in the low release rate greenhouses and 18 plants in the high release rate greenhouses had six leaves removed (two leaves from each stratum). Leaves were examined under a dissecting microscope in the laboratory and the numbers of live nymphs and pupae determined. Similar estimates were made for 72 poinsettias observed in five retail outlets in Amherst Massachusetts, in December 1994.

Results

Estimates of initial whitefly infestation on cuttings prior to potting

Initial infestation levels of eggs, nymphs, and adults of *B. argentifolii* on cuttings prior to potting did not differ statistically between plants used in the low and high release rate trials. Mean numbers of eggs per leaf were 0.03 ± 0.02 and 0.03 ± 0.01 respectively for the low and high release rate trials ($t = 0.16$, $df = 1076$, $P = 0.87$). Mean numbers of nymphs per leaf were 0.01 ± 0.004 and 0.01 ± 0.01 respectively for the low and high release rate trials ($t = 0.66$, $df = 1076$, $P = 0.51$). Mean numbers of adults per leaf were 0.02 ± 0.02 and

Table 1. Life-table for *Bemisia argentifolii* in the absence of *Eretmocerus eremicus* (unreplicated control greenhouse, low release rate trial, spring 1995).

	No. entering stage l_x			No. dying in stage d_x				No. deaths by factor			Marginal probability of mortality		
	Cohort			Cohort			Mortality factor	Cohort			Cohort		
Stage	1+2	3	4	1+2	3	4	f_{dx}	1+2	3	4	1+2	3	4
Egg/crawler	198	335	535	86	18	13	unknown death	86	18	13	0.43	0.05	0.02
First instar	112	317	522	17	13	6	unknown death	8	4	4	0.08	0.01	0.01
							disappearance	9	9	2	0.08	0.03	0.004
Second instar	95	304	516	1	1	8	unknown death	1	1	4	0.01	0.003	0.01
							disappearance	0	0	4	0.00	0.00	0.01
Third instar	94	303	508	2	3	14	unknown death	2	2	9	0.02	0.01	0.02
							disappearance	0	1	5	0.00	0.003	0.001
Fourth instar	92	300	494	1	2	14	unknown death	1	2	8	0.01	0.01	0.02
							disappearance						
Pupae	91	298	480	0	1	7	unknown death	0	1	3	0.00	0.003	0.01
							disappearance	0	0	4	0.00	0.00	0.01
Adults	91	297	473										

0.01 ± 0.003 respectively for the low and high release rate trial ($t = 1.01$, $df = 1076$, $P = 0.31$).

Life-tables for B. argentifolii *in the presence and absence of* E. eremicus

Life-tables for each whitefly cohort combined across replicated treatments are presented in tables 1–4. A summary life-table combining all whitefly cohorts across replicated treatments is presented in table 5. Survival of immature parasitoids after parasitism had been observed in photographs, and percent parasitism data for combined whitefly cohorts in parasitoid release greenhouses is given in table 6.

In the absence of parasitoids, marginal probability of mortality for unknown death was highest in the egg/crawler stage and lowest in the pupal stage for the low release rate control greenhouse (tables 1 and 5). In the high release rate control greenhouses, marginal probability of mortality for unknown death was highest in the egg/crawler stage and lowest in settled first and second instars (tables 3 and 5). Egg to adult whitefly survivorship was greatest in the unreplicated control greenhouse for the one female per plant per week release rate trial at 81% (tables 1 and 5). Egg to adult survivorship combined across whitefly cohorts for the two control greenhouses for the three females per plant per week release rate trial, was significantly lower (z-test for differences between population proportions) at 75% ($z = 3.66$, $P < 0.002$) (tables 3 and 5). In the absence of parasitoids, egg to adult survivorship for *B. argentifolii* increased across successive cohorts as poinsettia plants matured in the low release rate control greenhouse (table 1). In the high release rate control greenhouses, whitefly mortality tended to be lower in cohort 3 (table 3).

In the low release rate greenhouses, egg to adult survivorship averaged across both replicates was greatest in cohort 3 at 25%, lowest in cohorts 1+2 (2%), and intermediate in cohort 4 (9%) (table 2). Egg to adult survivorship averaged 12% across all cohorts for both low release rate greenhouses (tables 2 and 5). In the high release rate greenhouses, egg to adult survivorship averaged across both replicates was greatest in cohort 4 at 2%, and lowest in cohorts 1+2 and cohort 3 at 0.4% and 0.3%, respectively

Table 2. Combined life-table for *Bemisia argentifolii* across both greenhouse which received one female *Eretmocerus eremicus* per plant per week (low release rate trial, spring 1995 trial).

	No. entering stage l_x			No. dying in stage d_x				No. deaths by factor			Marginal probability of mortality		
	Cohort			Cohort			Mortality factor	Cohort			Cohort		
Stage	1+2	3	4	1+2	3	4	f_{dx}	1+2	3	4	1+2	3	4
Egg/crawler	353	475	638	95	22	75	unknown death	95	22	75	0.27	0.05	0.12
First instar	258	453	563	54	35	96	unknown death	51	28	86	0.20	0.06	0.02
							disappearance	3	7	10	0.01	0.02	0.02
Second instar	204	418	467	53	41	73	unknown death	53	38	70	0.26	0.09	0.15
							disappearance	0	3	3	0.00	0.01	0.01
Third instar	151	377	394	19	53	71	unknown death	19	52	68	0.13	0.14	0.17
							disappearance	0	1	3	0.00	0.003	0.01
Fourth instar	132	324	323	125	201	265	unknown death	47	54	52	0.67	0.23	0.29
							disappearance	1	2	2	0.01	0.01	0.01
							parasitized	77[a]	145[a]	211[a]	0.84	0.50	0.75
Pupae	7	123	58	1	4	1	unknown death	1	4	1	0.01	0.01	0.04
Adults	6	119	57										

[a]Parasitoid fate after parasitism was recorded photographically, see table 6.

Table 3. Combined life-table for *Bemisia argentifolii* across both greenhouses which did not receive *Eretmocerus eremicus* (high release rate trial, spring 1994).

	No. entering stage l_x			No. dying in stage d_x				No. deaths by factor			Marginal probability of mortality		
	Cohort			Cohort			Mortality factor	Cohort			Cohort		
Stage	1 + 2	3	4	1 + 2	3	4	f_{dx}	1 + 2	3	4	1 + 2	3	4
Egg / crawler	275	508	1007	35	36	115	unknown death	35	36	115	0.13	0.07	0.11
First instar	240	472	892	0	13	12	unknown death	0	11	6	0.00	0.02	0.01
							disappearance	0	2	6	0.00	0.004	0.01
Second instar	240	459	880	4	5	13	unknown death	4	4	7	0.02	0.01	0.01
							disappearance	0	1	6	0.00	0.002	0.01
Third instar	236	454	867	12	12	31	unknown death	11	11	22	0.05	0.02	0.03
							disappearance	1	1	9	0.004	0.002	0.01
Fourth instar	224	442	836	42	11	64	unknown death	42	10	62	0.19	0.02	0.07
							disappearance	0	1	2	0.00	0.002	0.002
Pupae	182	431	772	11	5	19	unknown death	11	2	14	0.06	0.005	0.02
							disappearance	0	3	5	0.00	0.01	0.01
Adults	171	426	753										

(table 4). Egg to adult survivorship averaged across all cohorts for both replicates was significantly higher in the low release rate greenhouses at 12% (cf. 0.9% for the high release rate greenhouses) ($z = 14.01$, $P < 0.002$) (tables 4 and 5).

The marginal probability for unknown death averaged across both low release rate greenhouses was consistently lower in cohort 3 for all lifestages (table 2). The marginal probability of mortality for parasitism was lowest in cohort 3 (table 2). In the high release rate greenhouses, the marginal probability for unknown death was highest in cohorts 1 + 2 for fourth instars and lowest for the egg / crawler stage. Marginal probability of mortality from unknown death decreased across successive cohorts for instars two to four (table 4). Marginal probability of mortality for parasitism increased across successive cohorts in high release rate greenhouses (table 4).

Survivorship curves

Survivorship curves (percentage entering successive lifestages as a fraction of the total number of eggs used to initiate combined cohorts) calculated from summary life-table data in table 5 for each experimental treatment are presented in fig. 1. Whitefly survivorship in control greenhouses was consistently higher for each developmental stage after the first instar when compared to the averaged survivorship across the replicated low and high release rate greenhouses. Survivorship curves for control greenhouses show highest real mortality (real mortality = d_i / l_c where d_i is death in the *i*th stage, and l_c is the size of the cohort at the commencement of the generation; real mortality for each lifestage is additive within a generation [Southwood, 1978]) occurring from egg to settled first instar (8–9%), thereafter, real mortality in successive lifestages was around 0–5% (table 5, fig. 1).

In the presence of *E. eremicus*, the number of nymphs surviving to enter successive developmental stages declined rapidly after settled first instar nymphs when compared to control greenhouses (fig. 1). In low release rate greenhouses, real mortality was greatest from fourth instar nymphs to pupae, where fourth instar mortality contributed 40% to the observed total mortality (table 5, fig. 1). In the high release

Table 4. Combined life-table for *Bemisia argentifolii* across both greenhouses which received three female *Eretmocerus eremicus* per plant week (high release rate trial, spring 1994).

	No. entering stage l_x			No. dying in stage d_x				No. deaths by factor			Marginal probability of mortality		
	Cohort			Cohort			Mortality factor	Cohort			Cohort		
Stage	1 + 2	3	4	1 + 2	3	4	f_{dx}	1 + 2	3	4	1 + 2	3	4
Egg / crawler	263	936	672	43	430	173	unknown death	43	430	173	0.16	0.46	0.26
First instar	220	506	499	117	316	179	unknown death	112	312	176	0.52	0.62	0.35
							disappearance	5	4	3	0.02	0.01	0.01
Second instar	103	190	320	72	126	105	unknown death	72	126	103	0.70	0.68	0.32
							disappearance	0	0	2	0.00	0.00	0.01
Third instar	31	64	215	21	25	73	unknown death	21	23	73	0.68	0.37	0.34
							disappearance	0	2	0	0.00	0.03	0.00
Fourth instar	10	39	142	9	36	130	unknown death	5	16	31	0.72	0.70	0.45
							disappearance	0	3	0	0.00	0.08	0.00
							parasitized	4[a]	17[a]	99[a]	0.64	0.72	0.85
Pupae	1	3	12	0	0	0							
Adults	1	3	12										

[a]Parasitoid fate after parasitism was recorded photographically, see table 6.

Table 5. Summary life-table for *Bemisia argentifolii* in the absence (one greenhouse) and presence (two greenhouses) of one female *Eretmocerus eremicus* per plant per week, and absence (two greenhouses) and presence (two greenhouses) of three female *E. eremicus* per plant per week.

	No. entering stage l_x				No. dying in stage d_x				Mortality factor	No. deaths by factor				Marginal probability of mortality			
Stage	[1]Con	[2]Con	[3]Rel	[4]Rel	[1]Con	[2]Con	[3]Rel	[4]Rel	f_{dx}	[1]Con	[2]Con	[3]Rel	[4]Rel	[1]Con	[2]Con	[3]Rel	[4]Rel
Egg/crawler	1068	1790	1466	1871	117	186	192	646	unknown death	117	186	192	646	0.11	0.10	0.13	0.35
First instar	951	1604	1274	1225	36	25	185	612	unknown death	16	17	165	600	0.02	0.01	0.13	0.49
									disappearance	20	8	20	12	0.02	0.005	0.02	0.01
Second instar	915	1579	1089	613	10	22	167	303	unknown death	6	15	161	300	0.01	0.01	0.15	0.49
									disappearance	4	7	6	3	0.004	0.004	0.01	0.01
Third instar	905	1557	922	310	19	55	143	119	unknown death	13	44	139	117	0.01	0.03	0.15	0.38
									disappearance	6	11	4	2	0.01	0.01	0.04	0.01
Fourth instar	886	1502	779	191	17	117	591	175	unknown death	11	114	153	52	0.01	0.08	0.31	0.53
									disappearance	6	3	5	3	0.01	0.002	0.01	0.02
									parasitized	0	0	433	120	0.00	0.00	0.65	0.82
Pupae	869	1385	188	16	8	35	6	0	unknown death	4	27	6	0	0.005	0.02	0.03	0.00
									disappearance	4	8	0	0	0.005	0.01	0.00	0.00
Adults	861	1350	182	16													

[1]One control greenhouse (no parasitoid releases) for the one female parasitoid per plant per week trial (low release rate trial), spring 1995.
[2]Two control greenhouses (no parasitoid releases) for the three female parasitoids per plant per week trial (high release rate trial), spring 1994.
[3]Two low release rate greenhouses (one female parasitoid per plant per week), spring 1995 trial.
[4]Two high release rate greenhouses (three female parasitoids per plant per week), spring 1994 trial.

rate greenhouses, real mortality was greatest from egg/crawler to settled first instar nymphs, where egg/crawler mortality accounted for 35% of the observed total mortality (table 5, fig. 1). Headrick *et al.* (1995, 1996) have reported that female *E. eremicus* will attack crawlers, and that first instar nymphs are lifted off leaves as a result of ovipositor probing. The largest observed real mortality difference between the low and high release rate greenhouses occurred in fourth instar nymphs where the percentage of individuals becoming adults differed by 31% (i.e. fourth instar mortality in the low release rate greenhouses was 40% of total observed mortality vs. 9% for the high release rate greenhouses) (fig. 1).

Net reproductive rates (R_o)

Sex ratio, net fecundity (L_xM_x), and net reproductive rate (R_o) estimates for each whitefly cohort photographed in each treatment are presented in table 7. Temperatures in the spring 1994 trial (three females per plant per week) and the spring 1995 trial (one female per plant per week) increased over the course of the 14 weeks (table 7). Higher temperatures result in sex ratios with a higher proportion of females with higher net fecundity (Enkegaard, 1993). As a consequence of this rise in temperature, R_o estimates for successive whitefly cohorts in the low release rate control greenhouse (unreplicated) increased, and averaged 26.1 over the cropping cycle (table 7). In low release rate greenhouses, R_o values were highest in cohort 3, lowest in cohorts 1 + 2, and intermediate in cohort 4. In low release rate greenhouses, *B. argentifolii* had an average R_o of 3.7, reflecting a 86% decrease from the growth rate of the control population (table 7).

R_o estimates for successive whitefly cohorts in the high release rate control greenhouses increased and averaged 20.5 over the 14 week cropping period (table 7). In high parasitoid release rate greenhouses, R_o values were highest for cohort 4, and averaged 0.25 across all cohorts, a 98.8% decrease from the growth rate of the control population (table 7).

Trends in whitefly population density

Weekly population trends averaged across replicated treatments for live nymphs and pupae in the presence and absence of *E. eremicus* are presented in fig. 2. In the absence of parasitoids, densities of live nymphs and pupae increase

Table 6. Parasitoid (*Eretmocerus eremicus*) fate after parasitism was recorded photographically.

Parasitoid release rate	Cohort	% Emerged	% Undetermined	% Disappeared	% Died	% Parasitism[1]
1 female/plant/week	1 + 2	69	27	3	1	30
(low release rate trial)	3	82	8	3	6	32
	4	50	46	3	1	37
						Average % parasitism[1]: 34
3 females/plant/week	1 + 2	0	50	0	50	2
(high release rate trial)	3	0	94	6	0	3
	4	28	62	6	4	20
						Average % parasitism: 10

[1]Average % parasitism = total no. parasitized nymphs/total number of settled first instars across all cohorts × 100.

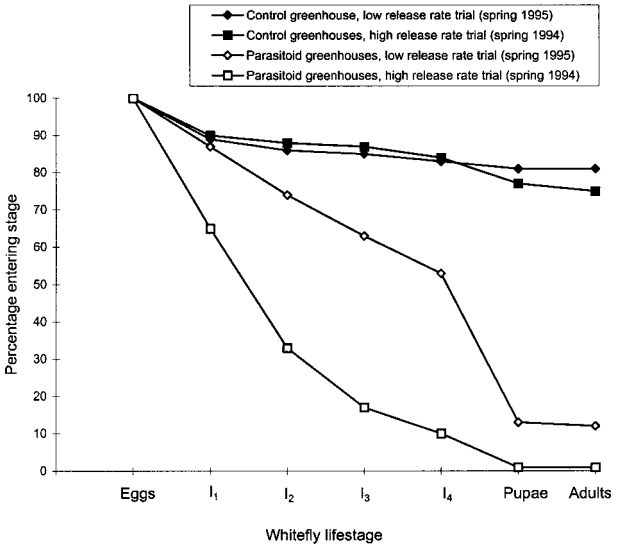

Fig. 1. Survivorship curves for *Bemisia argentifolii* cohorts on poinsettia in the presence and absence of *Eretmocerus eremicus*. Percentage entering each stage was calculated from the number in that particular lifestage divided by the number of eggs used to initiate that particular cohort. Data used were from table 5 (I_1 = settled first instar, I_2 = second instar, I_3 = third instar, I_4 = fourth instar).

rapidly in number after week 11 (fig. 2A). Densities of immature whiteflies in the unreplicated low release rate control greenhouse (spring 1995) increased more rapidly than the replicated high release rate control greenhouses (spring 1994). This is attributable to greater egg to adult survivorship in the control greenhouse for the low release rate trial (table 5), and a higher proportion of adults being females with higher net fecundity. These effects were due to higher temperatures in the control greenhouse for the low release rate trial over the 14 week test (table 7). At week 14, the numbers of live nymphs and pupae per plant were 1.2 times larger in the low release rate control greenhouse than in the high release rate control greenhouses.

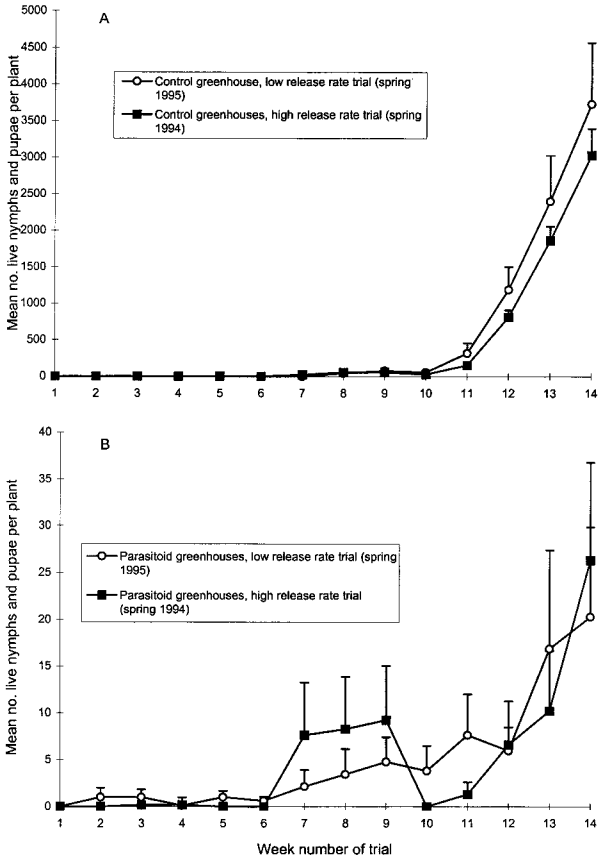

Fig. 2. Mean number of live nymphs and pupae (±SEM) per poinsettia plant in the control (A) and parasitoid release (B) greenhouses at a low release rate (one female *Eretmocerus eremicus* per plant per week), and a high release rate trial (three female *E. eremicus* per plant per week).

Bemisia argentifolii population trends in the low and high release rate greenhouses were similar. At week 14, the average numbers of live immature whitefly nymphs and pupae per plant in the high release rate greenhouses was 1.3

Table 7. Mean temperature ±SE, sex ratio, net fecundity (L_xM_x), and net reproduction (R_o) estimates for *Bemisia argentifolii* in each experimental greenhouse.

Greenhouse	Cohort	Temp.	Sex ratio	No. eggs	No. adults	No. females	Net fecundity	Net reproductive rate
Low release control	1 + 2	22.8 ± 0.4	0.66	198	91	60	42.6	12.9
greenhouse (spring 1995)	3	23.9 ± 0.5	0.68	335	297	201	49.5	29.7
	4	24.3 ± 0.4	0.68	535	473	324	52.3	31.7
Low control average	1–4	23.7 ± 0.2	0.67	1068	861	580	48.1	26.1
Low release rate	1 + 2	22.4 ± 0.3	0.65	353	6	4	40.2	0.4
greenhouse (spring 1995)	3	23.2 ± 0.2	0.67	473	119	79	45.4	7.6
	4	23.7 ± 0.3	0.67	638	57	38	48.4	2.9
Low release average	1–4	23.1 ± 0.2	0.66	1466	182	121	44.6	3.7
High release control	1 + 2	21.6 ± 0.2	0.64	275	171	109	35.1	13.9
greenhouse (spring 1994)	3	22.4 ± 0.3	0.65	508	426	277	39.7	21.6
	4	23.9 ± 0.4	0.68	1007	753	510	49.5	25.0
High control average	1–4	22.6 ± 0.2	0.65	1790	1350	883	41.5	20.5
High release rate	1 + 2	21.8 ± 0.2	0.64	263	1	1	35.9	0.1
greenhouses (spring 1994)	3	21.8 ± 0.3	0.64	936	3	2	36.5	0.1
	4	24.6 ± 0.5	0.69	672	12	8	54.1	0.7
High release average	1–4	22.9 ± 0.2	0.66	1871	16	11	43.6	0.3

times higher than the low release rate greenhouses, and 0.9% that of the corresponding control greenhouse. At the same time in the low release rate greenhouses, the average number of live nymphs and pupae per plant was 0.5% that of the corresponding control greenhouses.

Trends in percentage parasitism and numbers of emerging parasitoids

Percent nymphs parasitized, parasitoid emergence patterns, and estimates of total numbers of females emerging into the low and high release rate greenhouses are shown in fig. 3. In low release rate greenhouses, percent parasitism steadily increased after week 9 to reach 100% at weeks 13 and 14 (fig. 3A). Parasitoid emergence in the low release rate greenhouses began in week 8 and peaked at weeks 11 and 14. At week 14, estimates of the numbers of females emerging into the low release rate greenhouses was 2.2 times that of the weekly release rate (fig. 3A). In high release rate greenhouses, successful parasitism and parasitoid emergence was not observed on tagged leaves used for population counts (fig. 3B). However, parasitism and parasitoid emergence was observed in artificial cohorts photographed for life-table

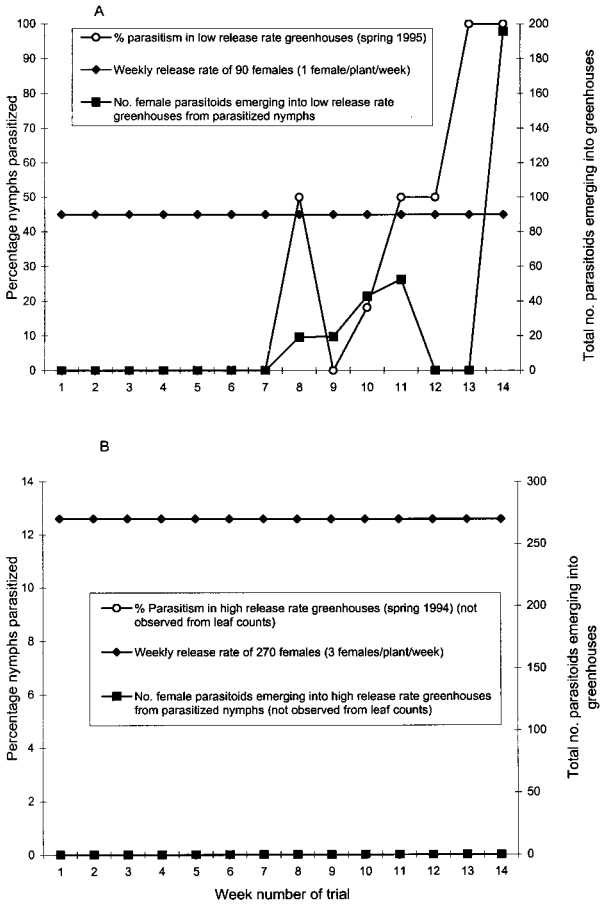

Fig. 3. Average weekly estimates of the percentage of *Bemisia argentifolii* nymphs parasitized by *Eretmocerus eremicus* in the low (A) and high (B) release rate greenhouses and the total number of *E. eremicus* emerging weekly into the low (A) and high (B) release rate greenhouses.

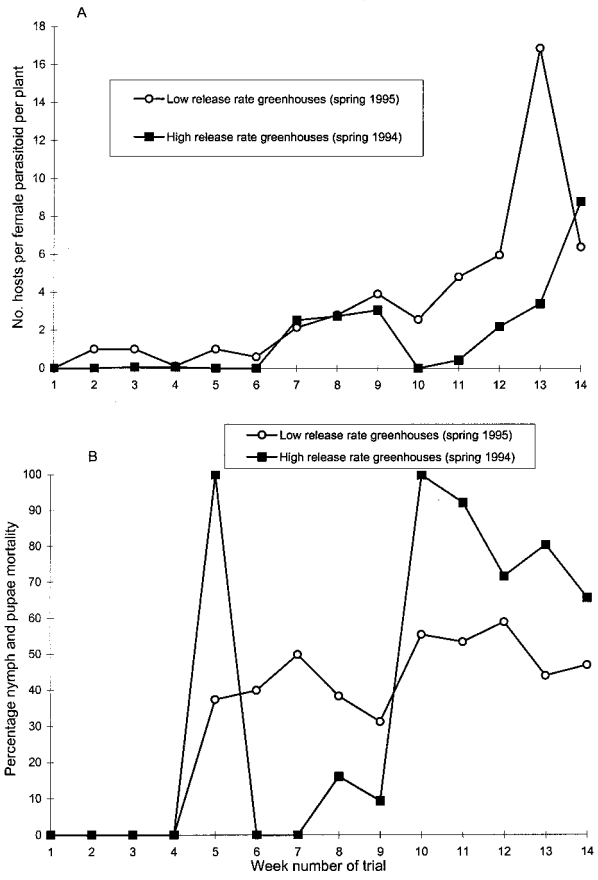

Fig. 4. The number of susceptible *Bemisia argentifolii* nymphs and pupae per plant (A) available for host feeding and parasitism by individual female parasitoids (*Eretmocerus eremicus*) for the low and high release rate greenhouses; and (B) the percentage mortality of *B. argentifolii* nymphs and pupae in the presence of *E. eremicus* in the low and high release rate greenhouses.

construction. Failure to detect parasitism on tagged leaves may have resulted from mortality (e.g. host feeding of parasitized nymphs, encapsulation (Gerling *et al*., 1990, 1991), or superparasitism) of hosts before parasitism was observed.

Trends in host:parasitoid ratio and host mortality

The average number of nymphs per plant available for attack by individual parasitoids for each week of the trial in the low and high release rate greenhouses are shown in fig. 4A. Average weekly percent mortality trends (excluding parasitism) for *B. argentifolii* in the low and high release greenhouses are shown in fig. 4B.

For the first 6 weeks of the high release rate trial, there were no detectable susceptible stages available for attack by female parasitoids (fig. 4A). In the low release rate greenhouses, the numbers of susceptible hosts per plant increased after week 6 to peak at 16.9 hosts per parasitoid per plant at week 13 before declining to 6.4 hosts per parasitoid per plant at week 14 (fig. 4A). This observed decline occurred because of high parasitoid emergence at week 14 (fig. 3A). In high release rate greenhouses, numbers of susceptible hosts

per plant per week steadily increased after week 10 to reach 8.8 susceptible hosts per parasitoid per plant at week 14 (fig. 4A). A decline in the number of available hosts per parasitoid did not occur in the high release rate greenhouses because in-house reproduction and parasitoid emergence were negligible (fig. 3B). At week 14, the average number of hosts available for attack per parasitoid per plant was 1.4 times higher in the high release rate greenhouses when compared to low release rate greenhouses.

In low release rate greenhouses, percentage mortality averaged 45.7% $\pm$ 2.8% (SE) after week 5 (fig. 4B). In high release rate greenhouses, percentage mortality reached 100% in weeks 5 and 10 (fig. 4B). After week 10, percentage mortality decreased in the high release rate greenhouses (fig. 4B) as the numbers of live nymphs in the high release rate greenhouses increased (fig. 2B). At week 14, percentage mortality was 1.4 times higher in high release rate greenhouses when compared to low release rate greenhouses.

End of crop sales inspection

At sale (week 14), the mean number of live nymphs and pupae per leaf combined across replicated greenhouses were 1.13 $\pm$ 0.19 and 2.97 $\pm$ 0.59 respectively for the low and high release rate greenhouses. The mean number of live nymphs and pupae per leaf on plants inspected in retail outlets was 1.45 $\pm$ 0.36 (infestation data from retail outlets was collected before imidacloprid was registered for greenhouse use in Massachusetts) (table 8). The mean number of nymphs per leaf differed significantly between treatments ($F = 4.27$, $df = 827$, $P = 0.01$). There were more live nymphs per leaf in the high release rate greenhouses than in the low release rate greenhouses and on plants produced with insecticides. There was no significant difference between nymph numbers on leaves in the low release rate greenhouses and on chemically protected plants.

Immature whiteflies in the high release rate greenhouses were found on a larger percentage of plants than insecticide treated plants (table 8). The low release rate of *E. eremicus* produced a poinsettia crop with similar final numbers of live immature whiteflies as insecticide protected plants, but survivors were spread over a larger number of plants. A summary of infestation statistics for end of crop sales inspection are presented in table 8.

Discussion

In small experimental greenhouses at Cornell University, life-table analyses showed that *E. eremicus* released at one female per plant per week (low release rate) and three females per plant per week (high release rate) exerted a suppressive effect on *B. argentifolii* population growth on poinsettia when compared to greenhouses which did not receive the parasitoid (table 5, fig. 2A,B). There was substantial reduction in net reproductive rates of *B. argentifolii* in greenhouses (98.8% reduction in high release rate greenhouses and 86% in low release rate greenhouses) into which *E. eremicus* was released when compared to greenhouses which did not receive the parasitoid (table 7).

R_o estimates for each whitefly cohort in the high release rate greenhouses were <1.0 indicating declining population growth (Carey, 1993), however this trend was not reflected in the weekly population counts (fig. 2B). In the high release rate greenhouses, densities of immature whiteflies increased after week 10 (fig. 2B) so that at week 14 of the trial when the end of crop sales inspection was made, mean numbers of immature whiteflies on poinsettia leaves were significantly greater than those on leaves in the low release rate greenhouses (fig. 2B) and plants treated with insecticides (table 8). A possible reason for the observed discrepancy between life-table data and population counts in the high release rate greenhouses is the spatial distribution of hosts on poinsettia leaves.

At the high release rate (three females per plant per week), *E. eremicus* was very efficient at locating and killing large numbers (in excess of 99%) of whitefly nymphs in artificially created patches that were photographed (tables 4 and 5). A shortcoming of the photography method is that it fails to record the fates of whitefly nymphs dispersed over a large area. Photographed nymphs in this study were in a 805 mm^2 area (approx. 5% of the leaf's surface area), and it is possible that if similar numbers of nymphs were spread over a larger area of leaf, individual nymphs may not be found as readily by searching females, and *B. argentifolii* survivorship and R_o rates would be higher.

Burnett (1958) has shown that *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae), a parasitoid of greenhouse whitefly, *T. vaporariorum*, parasitized more nymphs in clumped distributions when compared to levels of parasitism for the same number of nymphs distributed uniformly. Also, with increasing numbers of searching females, superparasitism increased and individual females successfully parasitized fewer hosts. Similar results have been observed with a pteromelid parasitoid attacking a standard number of fly pupae exhibiting various degrees of aggregation in experimental arenas (Jones & Turner, 1987). *Eretmocerus eremicus* may process host patches in a similar way to *E. formosa*, and nymph mortality in patches with dispersed hosts may be less than in patches of similar densities containing aggregated nymphs. Consequently, low levels of aggregation on poinsettia leaves may provide *B. argentifolii* nymphs with refugia when *E. eremicus* is released inundatively in greenhouses. Kareiva (1990) suggests that a shortcoming with the majority of impact evaluations for natural enemies in the field is the lack of work assessing the

Table 8. Infestation statistics for live *Bemisia argentifolii* nymphs and pupae on poinsettia leaves from experimental greenhouses in which *Eretmocerus eremicus* had been released and on leaves of poinsettias collected from retail outlets at the end of the 1994 growing season (autumn).

Treatment	No. plants inspected	% Plants infested	No. leaves examined	% Leaves infested	Nymphs/leaf $\pm$ SE
Low release rate greenhouses	30	73	180	25	1.13 $\pm$ 0.19
High release rate greenhouses	36	83	216	32	2.97 $\pm$ 0.59
Five retail outlets in Amherst, Massachusetts	72	28	432	12	1.45 $\pm$ 0.36

spatial heterogeneity and the spatial dimension of pest and natural enemy distributions. Further work is needed to determine how the degree of host spatial aggregation on poinsettia leaves affects the intensity and pattern of host feeding and parasitism by *E. eremicus*.

In the high release rate greenhouses, when plants were of small to medium height, percent parasitism was low in cohorts 1 + 2 and 3, at 2–3% and mortality was high at 99.6–99.7% (tables 4 and 6). At this stage of the cropping cycle, and at the high release rate, host feeding was a major mortality factor, and the impact of the *E. eremicus* was similar to that of a predator. In cohort 4, when plants were large, percent parasitism increased to 20% and mortality was 98% (tables 4 and 6). Higher levels of parasitism may have occurred in cohort 4 because female parasitoids were foraging over a larger plant canopy and nymphs that were successfully parasitized were not subjected as frequently to either host feeding or superparasitism by conspecific females. Levels of parasitism that were detected in cohort 4 in high release rate greenhouses with photography were not observed in weekly population counts on tagged leaves (fig. 3B). Population counts may have more accurately captured parasitism trends if plants were selected at random in greenhouses each week, and leaves then randomly selected within strata.

Eretmocerus mundus Mercet (Hymenoptera: Aphelinidae) can discriminate between parasitized and unparasitized *B. tabaci* nymphs on cotton, and females avoid ovipositing in parasitized hosts (Foltyn & Gerling, 1985). Host discrimination by *E. mundus* may be mediated by female marking of hosts after oviposition. Similar mechanisms may be used by *E*. sp. nr. *californicus* attacking *T. vaporariorum* in Hawaii because superparasitism by this parasitoid in field collected material was rare (Foltyn & Gerling, 1985). Superparasitism by *E.* sp. nr. *californicus* attacking *B. tabaci* has been observed, but the developmental outcome of competing larvae was undetermined (Gerling *et al*., 1990). In the laboratory, *E. californicus* can be easily induced to superparasitize at low host:parasitoid ratios (Gerling, 1966). In our trials, when high release rates were employed, mechanisms which normally limit superparasitism and host feeding of parasitized nymphs may not have operated because of low host:parasitoid ratios when plants were small.

In the low release rate greenhouses, percent parasitism in whitefly cohorts was higher (table 6) and average percent parasitism across all cohorts was 3.4 times greater than the high release rate greenhouses (table 6). Poinsettia varieties differed between the low and high release rate trials with 'Freedom Red' and 'Celebrate II' used respectively. Trichome densities on poinsettia leaves can differ significantly between cultivars with less hirsute leaves facilitating greater attack rates by parasitoids on *B. argentifolii* nymphs (Heinz & Parrella, 1994). Trichome densities did not differ significantly between cultivars in this study (Sanderson, unpublished). However, parasitoid emergence rates can be significantly affected by cultivar (Heinz & Parrella, 1994) and this may have influenced observed parasitism levels in the low and high release rate trials. In-house reproduction and parasitoid emergence supplemented weekly releases after week 7 in the low release rate greenhouses (fig. 3A), and at week 14 the estimated number of females emerging into the low release greenhouses was 2.2 times that of the weekly release rate (fig. 3A). Weekly releases and in-house emergence of *E. eremicus* at week 14 of the low release rate trial was sufficient to reduce the number of live whitefly nymphs on poinsettia leaves to levels lower than those recorded in the high release rate greenhouses at week 14 when the end of crop sales inspection was made (table 8). High levels of in-house reproduction by *E. eremicus* at the low release rate has important implications for using this parasitoid in inundative release programmes.

Successful inundative biological control of *B. argentifolii* on poinsettia with *E. eremicus* is a complicated inter-play between: (i) weekly release rate; (ii) mortality from host feeding and superparasitism; (iii) levels of in-house reproduction by parasitoids; and (iv) increasing plant canopy. Maximizing parasitoid efficacy when used inundatively may require varying the release rate over the course of the growing season. When plants are small, the low release rate would promote parasitism in the early to mid part of the growing season. Increasing the release rate later in the growing season would augment the action of parasitoids born into the greenhouse and compensate for an increasing plant canopy. This could minimize the number of nymphs escaping attack and improve control. A variable release strategy which maximizes in-house reproduction and host feeding by *E. eremicus* could result in cost-effective control with this biological control agent. We are currently analysing the results of variable release rate trials with *E. eremicus* for control of *B. argentifolii* on poinsettia.

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