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Biological Control of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on Poinsettia with Inundative Releases of *Encarsia formosa* (Hymenoptera: Aphelinidae): Are Higher Release Rates Necessarily Better?

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The effectiveness of inundative releases of the parasitoid *Encarsia formosa* for control of *Bemisia argentifolii* on poinsettia was determined in replicated experimental greenhouses. We evaluated two release rates of *E. formosa:* a low release rate (1 wasp/plant/week, released in two greenhouses, in spring 1995) and a high release rate (3 wasps/plant/week, released in two greenhouses, in fall 1993), each over a 14-week growing season. Each release trial had one or two control greenhouses in which *B. argentifolii* developed on poinsettia in the absence of *E. formosa.* Life-tables were constructed for *B. argentifolii* in the presence and absence of *E. formosa* by using a photographic technique to follow cohorts of whiteflies on poinsettia leaves. Weekly population counts of the whitefly were also made. In the absence of *E. formosa,* egg to adult survivorship of *B. argentifolii* on poinsettia was 75–81%. At the low release rate, egg to survivorship of *B. argentifolii* was 5% and parasitism was 13%. At the high release rate, egg to adult survivorship for *B. argentifolii* was 8% and parasitism was 23%. The net reproductive rates (R_0) for *B. argentifolii* populations in the absence of *E. formosa* ranged from 18.01–26.12, indicating a rapidly increasing population. Net reproductive rates for whitefly populations subject to wasp releases were 1.54 for the low release rate greenhouses and 2.11 for the high release rate greenhouses, indicating substantially reduced *B. argentifolii* population growth. The low release rate provided better control of *B. argentifolii* than the high release rate. This difference was attributed to higher levels of mortality of whiteflies at the low release rate in the first 5–6 weeks of the growing period. We suggest that mutual interference may also have affected observed levels of mortality and parasitism.

KEY WORDS: ***Bemisia argentifolii;*** **whitefly;** ***Encarsia formosa;*** **parasitoid; poinsettia; inundative biological control; mutual interference; life-tables.**

INTRODUCTION

The silverleaf whitefly *Bemisia argentifolii* Bellows and Perring (=*Bemisia tabaci* (Gennadius) strain B) (Homoptera: Aleyrodidae) (Bellows *et al.,* 1994) is a serious pest on poinsettia worldwide. Presently, *B. argentifolii* is effectively controlled in the United States with a systemic chloronicotinyl insecticide, imidacloprid (Lopes, 1994). Due to widespread use of imidacloprid by greenhouse growers, development of resistance to this compound by *B. argentifolii* is expected (Cahill *et al.,* 1996). To reduce reliance on insecticides and delay resistance to effective insecticides, we have been evaluating the ability of parasitic wasps to control *B. argentifolii* on poinsettia. The purpose of this work has been to identify an efficacious parasitoid that can be used in an integrated pest management program for *B. argentifolii* on poinsettia (Hoddle and Van Driesche, 1996).

Encarsia formosa is a commercially available, uniparental, thelytokous parasitoid that is used worldwide to control greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), on greenhouse grown vegetable crops (van Lenteren and Woets, 1988). The ability of this wasp to control *B. argentifolii* on poinsettia in greenhouses is uncertain as published results differ in outcome (Albert and Sautter, 1989; Benuzzi *et al.,* 1990; Hoddle and Van Driesche, 1996; Parrella *et al.,* 1991; and Stenseth, 1993). We tested a high (3 wasps/plant/week) and low (1 wasp/plant/week) release rate of *E. formosa* for control of *B. argentifolii* on poinsettia. Our intention was to use these results as a standard against which to measure the efficacy of two other species of aphelinid wasps which are commercially available: *Eretmocerus eremicus* n. sp. Rose and Zolnerowich

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(Rose and Zolnerowich, 1997) and a strain of *Encarsia formosa* from Beltsville, MD.

We used replicated experimental greenhouses to construct paired life-tables for *B. argentifolii* on poinsettia in the presence and absence of *E. formosa*. Comparative life-table studies provide a powerful technique for such evaluations (Bellows *et al.*, 1992) because they provide detailed description of age-specific mortality of individuals in the population (Carey, 1993), and when information on the pest's fecundity is available, the effect of the natural enemy can be expressed in terms of its effect on the pest's population growth rate (Van Driesche and Bellows, 1996). Life-tables have been used previously to assess the effectiveness of biological control of whiteflies by aphelinid parasitoids (e.g., Summy *et al.*, 1984; Gould *et al.*, 1992; Hoddle and Van Driesche, 1996). In addition to life-table construction, we made weekly population counts of immature and adult *B. argentifolii* and parasitized whitefly nymphs on poinsettias in the experimental greenhouses.

Our objectives were to use life-tables and population counts to determine over the course of a 14-week poinsettia crop: (1) the suppressive effect of *E. formosa* on *B. argentifolii* population growth when compared to whitefly population growth in the absence of this natural enemy, and (2) if our low and high release rates of *E. formosa* differed in the level of control given.

MATERIALS AND METHODS

Experimental Greenhouses, Crop Management, and Initial Whitefly Infestation Levels

Evaluations of *E. formosa* were conducted in small, identical plastic greenhouses at Cornell University (Ithaca, NY). Each greenhouse ($5 \times 4 \times 3.5$ m) held six benches ($0.91 \times 1.5 \times 0.91$ m), each with 15 pots (15 cm diameter, with single stem poinsettias), for a total of 90 plants per greenhouse. The fall 1993 trial included two control greenhouses (no wasps released) and two wasp release greenhouses (3 wasps/plant/week). The spring 1995 trial included three greenhouses, one control greenhouse, and two wasp release greenhouses (1 wasp/plant/week). Four DDVP fumigant strips were hung in each control greenhouse to prevent parasitoid establishment. The poinsettia cultivar used for both tests was "Freedom Red," and each trial ran for 14 weeks.

The fall 1993 and spring 1995 poinsettia crops were each started from rooted cuttings received from Paul Ecke Ranch (Encinitas, CA), which had been produced without any use of systemic insecticides. After potting, plants were subjected to commercial management practices of fertilization (Peter's Exel [15-5-5] at 200 ppm, Peter's Stem at 0.01 g/liter, and MolyB liquid concentrate at 0.17 ml/liter), root rot control (Subdue [metalaxyl] applied at weeks 2 and 11 of each trial at a rate of 0.15 g/liter), and pinching (3 weeks after potting). Maximum and minimum temperatures were recorded daily.

For each trial, estimates of initial *B. argentifolii* densities on poinsettia cuttings from the supplier were made prior to potting by recording the number of nymphs and adults on each leaf of 102 randomly chosen cuttings.

Parasitoid Release Regimen

Encarsia formosa was evaluated at two release rates. The high release rate consisted of weekly releases of three females per plant, and the trial was conducted in fall 1993 (August 14 to November 19, 1993, 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). *Encarsia formosa* pupae were supplied by Bunting Biological North America (Oxnard, CA), and were shipped as parasitized *T. vaporariorum* nymphs glued to release cards. After receipt, wasps were allowed to emerge into petri dishes on the lids of which were thin streaks of honey as a food supplement. Prior to release, wasps were counted in petri dishes using a dissecting microscope in the laboratory. Petri dishes with wasps were then taken to greenhouses, distributed uniformly below the plant canopy, and opened. Wasps were released in this manner until the desired weekly release total had been achieved for each greenhouse.

Establishing and Photographing Whitefly Cohorts; Constructing Life-Tables and Survivorship Curves

The fates of cohorts of whitefly nymphs (2–99 whitefly nymphs) on poinsettia leaves were determined using a photographic technique, and the resultant photographic slides were used to construct life-tables for cohorts of *B. argentifolii* in the presence and absence of *E. formosa* (after Summy *et al.*, 1984; Gould *et al.*, 1992; and Hoddle *et al.*, 1996).

To establish a cohort of whiteflies, 10 to 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 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 subcohorts. Contemporary subcohorts within a greenhouse are collectively referred to as cohorts.

Egg numbers on all plants returned to greenhouses were standardized by removing eggs from sub-cohorts with a 000 size insect pin so that similar egg totals were

added to the greenhouses 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 thus occurred during, approximately, the first, second, and third whitefly generations, respectively. Eight to 10 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 chosen to be photographed. Photography commenced immediately after the nymphs in each sub-cohort had settled. Each sub-cohort was photographed twice on each examination date (an insurance measure for unfocused slides), and photography was repeated two times each week. Photography of a sub-cohort ceased when all the nymphs had died, disappeared, emerged as adult whiteflies, or produced adult parasitoids.

The camera used was a 35-mm SLR outfitted with a 55-mm macrolens, a dedicated ringflash, and one extension tube. F-stop and aperture settings were 16 and 22, respectively. The film used was 50asa color slide film.

Slides of each sub-cohort were analyzed in chronological order using a backlit 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.*, 1996, for more details on 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 greenhouse and these life-tables were combined across replicates. Summary life-tables for each treatment were obtained by pooling cohorts of nymphs over the entire cropping season and across replicates.

Survivorship curves for *B. argentifolii* were constructed from summary life-tables for each treatment. Percentage 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 observed disappearance rate. When disappearance and unknown death occurred contemporaneously, 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_0)

Sex ratio (females/males + females) for *B. argentifolii* on poinsettia is positively correlated with temperature. The relationship between sex ratio and temperature for this whitefly and plant, for the temperature range 19–28°C, is described by the equation SR = 0.018T + 0.247, $r^2 = 0.972$, where SR is sex ratio and *T* is temperature (Enkegaard, 1993a). 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 = 6.3474T − 102.11, $r^2 = 0.968$, 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_0) is the per capita average number of female offspring born to a cohort of females during their lifetime, and describes the growth rate of

the population (Carey, 1993). Sex ratio and net fecundity estimates were calculated as described above, and R_0 were calculated by dividing the theoretical fecundity of females emerging from photographed cohorts by the number of eggs used to establish those cohorts. Values of $R_0 < 1$ indicate a declining population, $R_0 > 1$ an increasing population, and $R_0 = 1$ a stable population (Carey, 1993).

Monitoring Bemisia argentifolii Population Densities

Population counts of immature and adult whiteflies on poinsettia leaves were made weekly. Numbers of first/second, third, and fourth instar nymphs, pupae, pupal 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, together with whitefly counts per leaf, to determine the mean number of whiteflies (by life stage) per plant on each sample date for each treatment.

Estimating In-House Parasitoid Reproduction

The number of wasps emerging each week into the greenhouse via in-house reproduction was calculated from the weekly estimates of numbers of whitefly cadavers from which wasps had emerged. Estimates of the number of newly emerged wasps 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 wasps for the greenhouse as a whole. Since whitefly cadavers from which wasps had emerged accumulated on leaves, each weekly estimate had the count from the preceding week subtracted to give net estimates of wasps emerging into the greenhouse. Parasitoids emerging from *B. argentifolii* live for approximately 8 days (Szabo *et al.*, 1993). To estimate the number of parasitoids in greenhouses each week we assumed females lived for 7 days only.

Estimating the Number of Hosts Available per Plant for Wasp Attack

Encarsia formosa will parasitize second, third, and fourth instars, and will host feed on all immature lifestages including pupae (Boisclair *et al.*, 1990; Enkegaard, 1993b). The number of susceptible hosts per plant available for attack by wasps (averaged for each treatment, for each week of the trial) was calculated by summing the per plant densities of the susceptible whitefly stages. The host/wasp ratio was then calculated by dividing the weekly estimate of susceptible stages by the estimated number of wasps per plant in the greenhouse. To estimate the number of wasps present in each greenhouse in specific weeks, the number of wasps released each week was added to the estimated number of wasps emerging from in-house wasp reproduction.

Estimating Percentage Mortality and Percentage Parasitism in Experimental Greenhouses

Average percentage mortality (excluding parasitism) and parasitism estimates in each week of each trial were estimated for each wasp release treatment from the weekly *B. argentifolii* population counts.

End of Crop Sales Inspection

At week 14 of the trial, 15 randomly selected plants in each of the wasp release houses had six leaves removed (two leaves from each stratum) and examined under a dissecting microscope in the laboratory for live nymphs and pupae. Numbers of live nymphs and pupae recorded were compared to similarly collected data from 112 poinsettias observed at five retail outlets in Amherst, Massachusetts, in December 1993.

RESULTS

Estimates of Initial Whitefly Infestation on Cuttings Prior to Potting

Initial *B. argentifolii* infestation on cuttings prior to potting did not differ statistically between the low and high release rate trials for eggs, nymphs, and adults. Mean numbers of eggs ($\pm$SE) per leaf were 0.03 ± 0.02 and 0.03 ± 0.02, respectively, for the low and high release rate trials ($t_{\text{value}} = 0.22$, $df = 1040$, $P = 0.83$). Mean numbers of nymphs per leaf ($\pm$SE) was 0.01 ± 0.01 and 0.00 ± 0.00, respectively, for the low and high

TABLE 1

Life-Table for *Bemisia argentifolii* in the Absence of *Encarsia formosa* (Unreplicated Control Greenhouse, Spring 1995 Trial)

	[1]l_x			[1]d_x				No. deaths by factor			Marginal probability of mortality		
Stage	[2]C_{1+2}	C_3	C_4	C_{1+2}	C_3	C_4	[1]f_{dx}	C_{1+2}	C_3	C_4	C_{1+2}	C_3	C_4
Egg/crawler	198	335	535	86	18	13	Unknown death	86	18	13	0.43	0.05	0.02
Settled [3]I_1	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
I_2	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
I_3	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	0.01
I_4	92	300	494	1	2	14	Unknown death	1	2	8	0.01	0.01	0.02
							Disappearance	0	0	6	0.00	0.00	0.01
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[a]	297[b]	473[c]										

[1] l_x, Number entering the stage. d_x, Number dying in the stage. f_{dx}, Factor responsible for observed mortality. See Southwood, 1978, and Carey, 1993, for more information on parts of life-tables.

[2] C_{1+2}, Cohorts 1 + 2 (established weeks 1 and 2); C_3, cohort 3 (established week 5); C_4, cohort 4 (established week 9).

[3] I_1, *B. argentifolii* first instar, I_2, second instar; I_3, third instar, I_4, fourth instar.

[a,b,c] Egg to adult survivorship for *B. argentifolii:* [a] 46%, [b] 89%, [c] 88%. Average egg to adult survivorship for *B. argentifolii* in the absence of *E. formosa* releases was 81%.

release rate trial ($t_{value} = 1.93$, $df = 1040$, $P = 0.05$). Mean numbers of adults per leaf (±SE) were 0.02 ± 0.02 and 0.00 ± 0.00, respectively, for the low and high release rate trials ($t_{value} = 1$, $df = 1040$, $P = 0.34$).

Life-Tables for B. argentifolii in the Presence and Absence of E. formosa

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

In the absence of parasitoids, whitefly mortality was highest in the egg/crawler stage and lowest in the pupal stage (Tables 1, 3, and 5). Egg to adult whitefly

TABLE 2

Combined Life-Table (Two Replicates) for *Bemisia argentifolii* Which Received One *Encarsia formosa* per Plant per Week (Low Release Rate Trial, Spring 1995)

	l_x			d_x				No. deaths by factor			Marginal probability of mortality		
Stage	C_{1+2}	C_3	C_4	C_{1+2}	C_3	C_4	f_{dx}	C_{1+2}	C_3	C_4	C_{1+2}	C_3	C_4
Egg/crawler	365	469	638	61	47	82	Unknown death	61	47	82	0.17	0.10	0.13
Settled I_1	304	422	556	13	91	173	Unknown death	6	81	156	0.02	0.20	0.29
							Disappearance	7	10	17	0.02	0.02	0.03
I_2	291	331	383	33	100	175	Unknown death	33	97	173	0.11	0.30	0.45
							Disappearance	0	3	2	0.00	0.01	0.01
I_3	258	231	208	22	103	96	Unknown death	22	102	94	0.09	0.44	0.46
							Disappearance	0	1	2	0.00	0.004	0.01
I_4	236	128	112	136	124	111	Unknown death	45	84	74	0.25	0.91	0.96
							Disappearance	1	2	4	0.004	0.02	0.04
							Parasitized	90[a]	38[a]	33[a]	0.43	0.66	0.76
Pupae	100	4	1	27	4	1	Unknown death	26	4	1	0.26	1.00	1.00
							Disappearance	1	0	0	0.01	0.00	0.00
Adults	73[b]	0[c]	0[d]										

[a] Parasite fate after parasitism was recorded photographically; see Table 6. [b,c,d] Egg to adult survivorship for *B. argentifolii:* [b] 20%, [c] 0%, [d] 0%. Average egg to adult survivorship for *B. argentifolii* with the release of one *E. formosa* per plant per week (both low release rate greenhouses combined) was 5%.

TABLE 3

Combined Life-Table (Two Replicates) for *Bemisia argentifolii* in the Absence of the High Release Rate of *E. formosa* (Three Wasps/Plant/Week, Fall 1993 Trial)

	l_x			d_x				No. deaths by factor			Marginal probability of mortality		
Stage	C_{1+2}	C_3	C_4	C_{1+2}	C_3	C_4	f_{dx}	C_{1+2}	C_3	C_4	C_{1+2}	C_3	C_4
Egg/crawler	295	593	841	63	85	99	Unknown death	63	85	99	0.21	0.14	0.12
Settled I_1	232	508	742	8	15	14	Unknown death	4	12	9	0.02	0.02	0.01
							Disappearance	4	3	5	0.02	0.01	0.01
I_2	224	493	728	15	7	14	Unknown death	14	7	11	0.06	0.01	0.02
							Disappearance	1	0	3	0.004	0.00	0.004
I_3	209	486	714	5	23	13	Unknown death	5	23	9	0.02	0.05	0.01
							Disappearance	0	0	4	0.00	0.00	0.01
I_4	204	463	701	13	36	15	Unknown death	13	35	13	0.06	0.08	0.02
							Disappearance	0	1	2	0.00	0.002	0.003
Pupae	191	427	686	2	9	3	Unknown death	2	9	3	0.01	0.02	0.004
Adults	189[a]	418[b]	683[c]										

[a,b,c] Egg to adult survivorship for *B. argentifolii:* [a] 64%, [b] 70%, [c] 81%. Average egg to adult survivorship for *B. argentifolii* in the absence of *E. formosa* releases (both high release rate control greenhouses combined) was 75%.

survivorship was greatest in the unreplicated control greenhouse for the low release rate trial (1995) at 81% (Tables 1 and 5). Egg to adult survivorship combined across whitefly cohorts for the two control greenhouses for the high release rate trial (1993) was significantly lower (*z* test for differences between population proportions) at 75% ($z = 3.66$, $z_{crit(0.05)} = 1.65$) (Tables 3 and 5). In the absence of parasitoids, egg to adult survivorship for *B. argentifolii* increased across successive cohorts as poinsettia plants matured (Tables 1 and 3).

In the low release rate greenhouses, egg to adult survivorship averaged across both replicates was greatest in cohorts 1 + 2 at 20% and declined to 0% in cohorts 3 and 4 (Table 2). Egg to adult survivorship averaged 5% 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 cohorts 1 + 2 at 26%, lowest in cohort 3 at 0.4%, and intermediate in cohort 4 at 6% (Table 4). Egg to adult survivorship averaged across all cohorts for both replicates was significantly higher in the high release greenhouses at 8% than that

TABLE 4

Combined Life-Table (Two Replicates) for *Bemisia argentifolii* Which Received Three *Encarsia formosa* per Plant per Week (High Release Rate Trial, Fall 1993)

	l_x			d_x				No. deaths by factor			Marginal probability of mortality		
Stage	C_{1+2}	C_3	C_4	C_{1+2}	C_3	C_4	f_{dx}	C_{1+2}	C_3	C_4	C_{1+2}	C_3	C_4
Egg/crawler	254	450	878	44	103	123	Unknown death	44	103	123	0.17	0.23	0.14
Settled I_1	210	347	755	4	59	131	Unknown death	3	50	117	0.01	0.14	0.15
							Disappearance	1	9	14	0.005	0.03	0.02
I_2	206	288	624	18	107	175	Unknown death	16	106	173	0.08	0.37	0.28
							Disappearance	2	1	2	0.01	0.003	0.003
I_3	188	181	449	23	59	114	Unknown death	23	59	113	0.12	0.33	0.25
							Disappearance	0	0	1	0.00	0.00	0.002
I_4	165	122	335	79	113	279	Unknown death	56	60	57	0.37	0.75	0.31
							Disappearance	0	0	2	0.00	0.00	0.01
							Parasitized	23[a]	53[a]	220[a]	0.17	0.71	0.76
Pupae	86	9	56	20	7	0	Unknown death	20	5	0	0.23	0.71	0.00
							Disappearance	0	2	0	0.00	0.22	0.00
Adults	66[b]	2[c]	56[d]										

[a] Parasite fate after parasitism has been recorded photographically; see Table 6. [b,c,d] Egg to adult survivorship for *B. argentifolii:* [b] 26%, [c] 0.4%, [d] 6%. Average egg to adult survivorship for *B. argentifolii* with the release of three *E. formosa* per plant per week (both high release rate greenhouses combined) was 8%.

TABLE 5

Summary Life-Tables Across Cohorts for *Bemisia argentifolii* in the Absence (One Greenhouse) and Presence (Two Greenhouses) of One *Encarsia formosa* per Plant per Week, and Absence (Two Greenhouses) and Presence (Two Greenhouses) of Three *E. formosa* per Plant per Week

	l_x				d_x					No. deaths by factor				Marginal probability of mortality			
Stage	[1]C_1	[2]C_3	[3]R_1	[4]R_3	C_1	C_3	R_1	R_3	f_{dx}	C_1	C_3	R_1	R_3	C_1	C_3	R_1	R_3
Egg/crawler	1068	1729	1472	1582	117	247	190	270	Unknown death	117	247	190	270	0.11	0.14	0.13	0.17
Settled I_1	951	1482	1282	1312	36	37	277	194	Unknown death	16	20	243	170	0.02	0.01	0.19	0.13
									Disappearance	20	17	34	24	0.02	0.01	0.03	0.02
I_2	915	1445	1005	1118	10	36	308	300	Unknown death	6	32	303	295	0.01	0.02	0.30	0.27
									Disappearance	4	4	5	5	0.004	0.003	0.005	0.004
I_3	905	1409	697	818	19	41	221	196	Unknown death	13	37	218	195	0.01	0.03	0.31	0.24
									Disappearance	6	4	3	1	0.01	0.003	0.004	0.001
I_4	886	1368	476	622	17	64	371	471	Unknown death	11	61	203	173	0.01	0.04	0.57	0.41
									Disappearance	6	3	7	2	0.01	0.002	0.01	0.003
									Parasitized	0	0	161[a]	296[b]	0.00	0.00	0.48	0.59
Pupae	869	1304	105	151	8	14	32	27	Unknown death	4	14	31	25	0.01	0.01	0.30	0.16
									Disappearance	4	0	1	2	0.01	0.00	0.01	0.01
Adults	861[c]	1290[d]	73[e]	124[f]													

[1] One control greenhouse (no wasp releases) for the one wasp per plant per week trial, spring 1995.
[2] Two control greenhouses combined across all cohorts for the three wasps per plant per week trial, fall 1993.
[3] Two low release rate greenhouses combined across all cohorts (one wasp per plant per week), spring 1995 trial.
[4] Two high release rate greenhouses combined across all cohorts (three wasps per plant per week), fall 1993 trial.
[a,b] % Parasitism (total no. parasitized in all cohorts/no. settled I_1 in all cohorts): [a] 13%, [b] 23%.
[c,d,e,f] Egg to adult survivorship for *B. argentifolii* across all cohorts: [c] 81%, [d] 75%, [e] 5%, [f] 8%.

in the low release rate treatment ($z = 3.24$, $z_{crit(0.05)} = 1.65$) (Tables 4 and 5).

The marginal probability of mortality for unknown death averaged across both low release rate greenhouses increased across successive whitefly cohorts for instars 1–4, as did the marginal rate of mortality for parasitism (Table 2). In the high release rate greenhouses, the observed trend was different, with the marginal probability of mortality from unknown death generally being greatest in cohort 3 for instars 1–4 and pupae, respectively (Table 4).

The smallest difference in unknown death between the control greenhouses and wasp release greenhouses across all cohorts, replicates, and treatments was in the egg/crawler stage, where unknown death was 1.2× lower in both control treatments than the respective

TABLE 6

Parasitoid Fate (*Encarsia formosa*) after Parasitism Was Identified in Photographic Slides

Wasp release rate	Cohort	% Emerged[a]	% Undetermined[b]	% Disappeared[c]	% Died [d]	% Parasitism[e]
1 Wasp/plant/week (Low release rate trial)	1 + 2	60	27	1	12	30
	3	45	47	0	8	9
	4	45	48	3	3	6
						Average % parasitism[f]: 13
3 Wasps/plant/week (High release rate trial)	1 + 2	57	22	0	22	11
	3	79	13	2	6	15
	4	24	67	2	7	29
						Average % parasitism: 23

[a] Emergence of parasitoid recorded photographically.
[b] Photography of parasitized whitefly ceased before developmental outcome was determined.
[c] Parasitized whitefly disappeared before developmental fate was determined.
[d] Parasite died inside host.
[e] % Parasitized was calculated as total no. nymphs parasitized across both replicates/total no. of settled first instars in that particular cohort across both replicates.
[f] Average % parasitism, total no. parasitized nymphs across all cohorts and replicates/total no. of settled first instars across all cohorts and replicates.

wasp release rate greenhouses (Table 5). The largest difference in unknown death between the low release rate control greenhouse and the low release rate greenhouses was in the fourth instar, where mortality from unknown death was 57× higher in the low release rate greenhouses (Table 5). The largest difference in unknown death between the high release rate control greenhouses and the high release rate greenhouses was in the pupal stage, where mortality from unknown death was 16× higher in the high release rate greenhouses (Table 5).

Survivorship Curves

Survivorship curves (percentage entering successive lifestages) 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 ith 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 (11–14%); thereafter, real mortality in successive lifestages was around 1–4% (Table 5, Fig. 1).

In the presence of *E. formosa*, the number of nymphs surviving to enter successive developmental stages declined rapidly after the settled first instar when compared to the respective control greenhouses (Fig. 1). In low release rate greenhouses, real mortality was greatest from fourth instars to pupae, where fourth instar mortality contributed 25% to the observed total mortality (Table 5, Fig. 1). In high release rate greenhouses, real mortality was greatest from fourth instar to pupae, where fourth instar mortality accounted for 30% of the observed total mortality (Table 5, Fig. 1). The largest observed real mortality difference between the low and high release rate greenhouses occurred in the first instar where the percentage of individuals becoming second instars differed between release rates by 7% (i.e., first instar mortality in the low release rate greenhouses was 19% of total observed mortality vs 12% for the high release rate greenhouses) (Fig. 1).

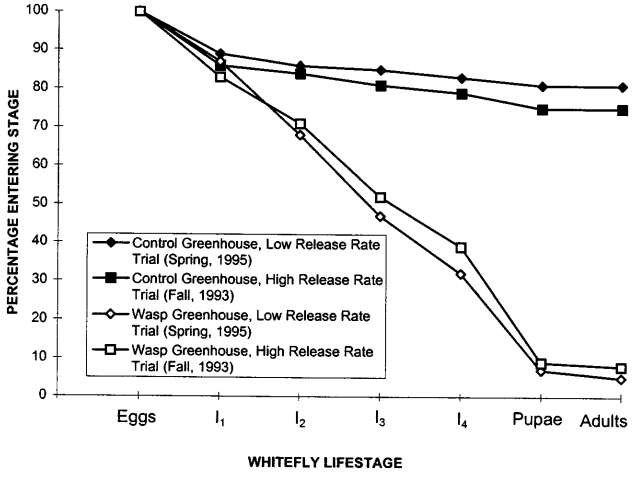

FIG. 1. Survivorship of *Bemisia argentifolii* cohorts on poinsettia in the presence and absence of *Encarsia formosa*. Survival rate for each stage was calculated as the number entering each lifestage divided by the number of eggs at the start of each cohort (see Table 5). I_1, Settled first instar; I_2, second instar; I_3, third instar; I_4, fourth instar.

Net Reproductive Rates (R_0)

Sex ratio, net fecundity (L_xM_x), and net reproductive rate (R_0) estimates for each whitefly cohort photographed in each treatment are presented in Table 7. Temperatures in the spring 1995 trial (1 wasp/plant/week) increased over the course of the fourteen weeks (Table 7). Higher temperatures result in sex ratios with a higher proportion of females with higher net fecundity (Enkegaard, 1993a). As a consequence of this rise in temperature, R_0 estimates for successive whitefly cohorts in the low release rate control greenhouse (unreplicated) increased and averaged 26.12 over the cropping cycle (Table 7). In low release rate greenhouses, R_0 values for each successive whitefly cohort decreased and *B. argentifolii* had an average R_0 of 1.54, reflecting a 94.1% decrease from the growth rate of the control population (Table 7).

Temperatures in the high release rate trial (3 wasps/plant/week, fall 1993) decreased over the course of the growing season. Lower temperatures result in sex ratios with a lower proportion of females and lower net fecundity of emerging females (Enkegaard, 1993a) (Table 7). R_0 estimates for successive whitefly cohorts in the high release rate control greenhouses decreased and averaged 18.01 over the 14-week cropping cycle (Table 7). In high wasp release rate greenhouses, R_0 values averaged 2.12, an 88.3% 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. formosa* are presented in Fig. 2. In the absence of parasitoids, densities of live nymphs and pupae increased rapidly in number after week 11 (Fig. 2A). Densities of immature whiteflies in the unrepli-

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

Greehouse	Cohort[1]	Temp[2]	Sex Ratio[3]	No. Eggs[4]	No. Adults[5]	No. Females[6]	L_xM_x[7]	R_o[8]
Low release control	1 + 2	22.79 ± 0.35	0.66	198	91	59.81	42.57	12.86
Greenhouse (spring, 1995)	3	23.89 ± 0.46	0.68	335	297	201.07	49.52	29.72
	4	24.33 ± 0.44	0.68	535	473	324.01	52.34	31.70
Low control average	1–4	23.67 ± 0.24	0.67	1068	861	579.51	48.14	26.12
Low release rate	1 + 2	23.45 ± 0.21	0.67	365	73	48.84	46.73	6.25
Greenhouses (spring, 1995)	3	23.87 ± 0.28	0.68	469	0	0.00	49.40	0.00
	4	24.26 ± 0.26	0.68	638	0	0.00	51.89	0.00
Low release average	1–4	23.41 ± 0.18	0.67	1472	73	48.79	46.48	1.54
High release control	1 + 2	24.32 ± 0.55	0.68	295	189	129.41	52.24	22.92
Greenhouses (fall, 1993)	3	21.58 ± 0.38	0.64	593	418	265.63	34.88	15.63
	4	20.61 ± 0.26	0.62	841	683	422.05	28.69	14.40
High control average	1–4	22.00 ± 0.32	0.64	1729	1290	829.47	37.53	18.01
High release rate	1 + 2	24.69 ± 0.57	0.69	254	66	45.64	54.64	9.82
Greenhouses (fall, 1993)	3	21.70 ± 0.31	0.64	450	2	1.28	35.64	0.10
	4	21.25 ± 0.18	0.63	878	56	35.25	32.77	1.32
High release average	1–4	22.59 ± 0.34	0.65	1581	124	81.05	41.28	2.12

[1] Cohort, whitefly cohort from life-table.
[2] Temp., average of the daily maximum and minimum temperatures ± SE experienced by each cohort across replicated treatments.
[3] Sex ratio, proportion of females produced at mean temperature experienced by each cohort (estimated from Enkegaard, 1993).
[4] No. Eggs, Total number of eggs in the cohort that was photographed (from life-tables).
[5] No. Adults, Total number of adults that were produced from the photographed eggs (from life-tables).
[6] No. Females, Estimated number of females in 5 using sex ratio estimate in 3.
[7] L_xM_x , net fecundity per female at mean temperature experienced by each whitefly cohort (estimated from Enkegaard, 1992).
[8] Net reproductive rate (R_o), the total number of progeny produced by emerged females (column 6 × column 7)/number of eggs that started that cohort (column 4).

cated low release rate control greenhouse (spring 1995) increased more rapidly than the replicated high release rate control greenhouses (fall 1993). This is attributable to greater egg to adult survivorship (Table 5), a more female-biased sex ratio, and higher fecundity in the low release rate control greenhouse, compared to the high release rate greenhouses, because of increasing temperatures (Table 7). At week 14, numbers of live nymphs and pupae per plant were 4.9× greater in the low release rate control greenhouse when compared to the high release rate control greenhouses.

The low release rate of *E. formosa* (1 wasp/plant/week) suppressed *B. argentifolii* population growth more effectively than the high release rate (3 wasps/plant/week) (Fig. 2B). After week 8, increased whitefly population growth was observed in both wasp release greenhouses and was greatest in the high wasp release rate greenhouses. Wasps in the low release rate greenhouses substantially reduced whitefly population growth after week 11 and this was not observed in the high release rate greenhouses (Fig. 2B). At week 14, the average numbers of live immature whitefly nymphs and pupae per plant in the high release rate greenhouses was 15× higher than the low release rate greenhouses and 5% that of the corresponding control greenhouses. At the same time, in the low release rate greenhouses, the average number of live nymphs and pupae per plant was 0.08% that of the corresponding control greenhouses.

Trends in Percentage Parasitism and Numbers of Emerging Parasitoids

Percentage nymphs parasitized, wasp emergence patterns, and estimates of total numbers of wasps emerging into the low and high release rate greenhouses are shown in Fig. 3. In low release rate greenhouses, three major peaks in parasitism were observed at weeks 5, 9, and 14 (Fig. 3A). Peak wasp emergence in the low release rate greenhouses occurred at weeks 7, 11, and 13, 2 weeks after peaks in parasitism were observed. Wasp emergence at week 13 was very close to the number of wasps released into the low release rate greenhouses that week. In-house reproduction by *E. formosa* during the trial may have contributed to whitefly population growth suppression, particularly after week 11, when a rapid decline in numbers of live whitefly nymphs and pupae was observed (Fig. 2A).

In the high wasp release rate greenhouses, parasitism was not observed until week 10 (as opposed to week 5 in the low release rate greenhouses) and peaked at week 11 (Fig. 3B). Wasp emergence occurred 2 weeks later at week 13, when emergence from in-house reproduction exceeded the weekly release rate (Fig. 3B). As

with the low release rate greenhouses, wasp emergence at this time may have contributed to the decline in live whitefly nymphs and pupae in the high release rate greenhouses after week 12 (Fig. 2B).

Trends in Host: Parasitoid Ratio and Host Mortality

The average numbers of nymphs per plant available for attack by individual wasps, for each week of the trial in the low and high release rate greenhouses, are shown in Fig. 4A. Average weekly trends in mortality from causes other than successful parasitism (i.e., host feeding and aborted parasitism) for *B. argentifolii* in the low and high release greenhouses are shown in Fig. 4B.

During the first 7 weeks of both trials, numbers of susceptible hosts available for attack per wasp were similar (Fig. 4A). However, percentage mortality was higher in the low release rate greenhouses over this time and reached 100% at weeks 5–7. Similar levels of mortality were not observed in the high release rate greenhouses (Fig. 4B). As the number of hosts available for attack increased after week 7 in both the low and high release rate greenhouses (Fig. 4A), whitefly mortality increased more rapidly (Fig. 4B), and numbers of live nymphs available for attack per wasp declined more quickly (Fig. 4A) in the low release rate greenhouses.

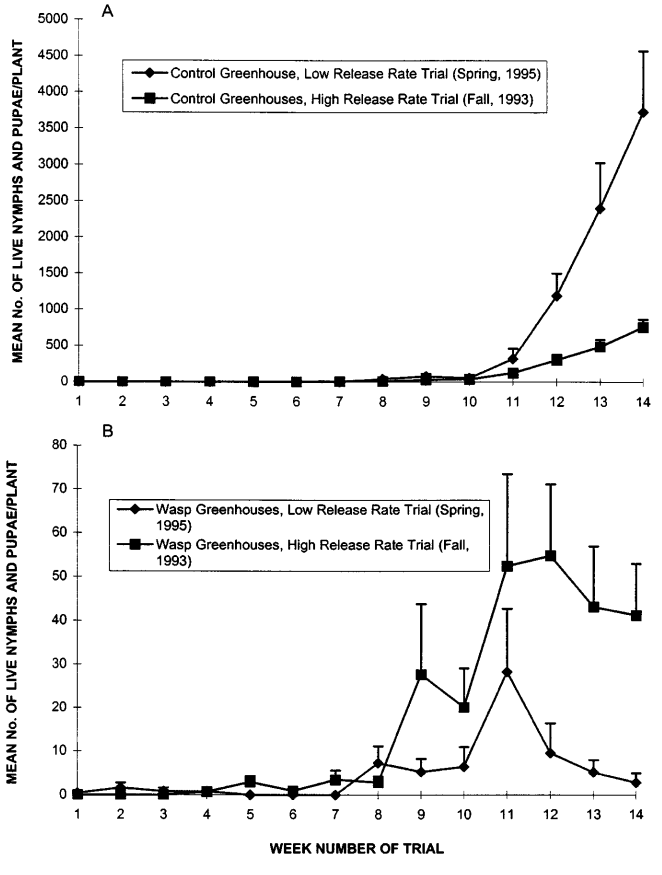

FIG. 2. Mean number of live nymphs and pupae (±SEM) per poinsettia plant in the control (A) and wasp release (B) greenhouses at a low release rate (1 wasp/plant/week), and a high release rate (3 wasps/plant/week).

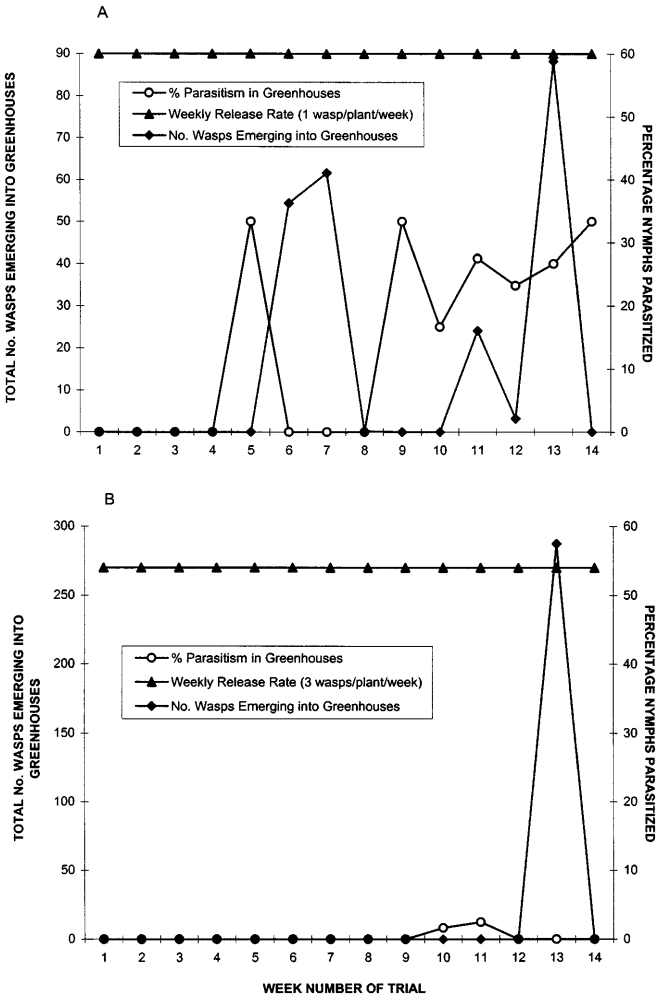

FIG. 3. Average weekly estimates of the percentage of *Bemisia argentifolii* nymphs parasitized by *Encarsia formosa* in the low (A) and high (B) release rate greenhouses and the total number of *Encarsia formosa* emerging weekly into the low (A) and high (B) release rate greenhouses.

At week 14, the average number of hosts available for attack per wasp per plant was 4.7× higher in the high release rate greenhouses, and percentage mortality was 1.6× higher in the low release rate greenhouses.

End of Crop Sales Inspection

At sale (week 14), the mean numbers of live nymphs and pupae (±SE) per leaf combined across replicated greenhouses were 0.09 ± 0.04 and 0.82 ± 0.29, 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 0.69 ± 0.20. (Infestation data from retail outlets was collected before imidacloprid was registered for greenhouse use in

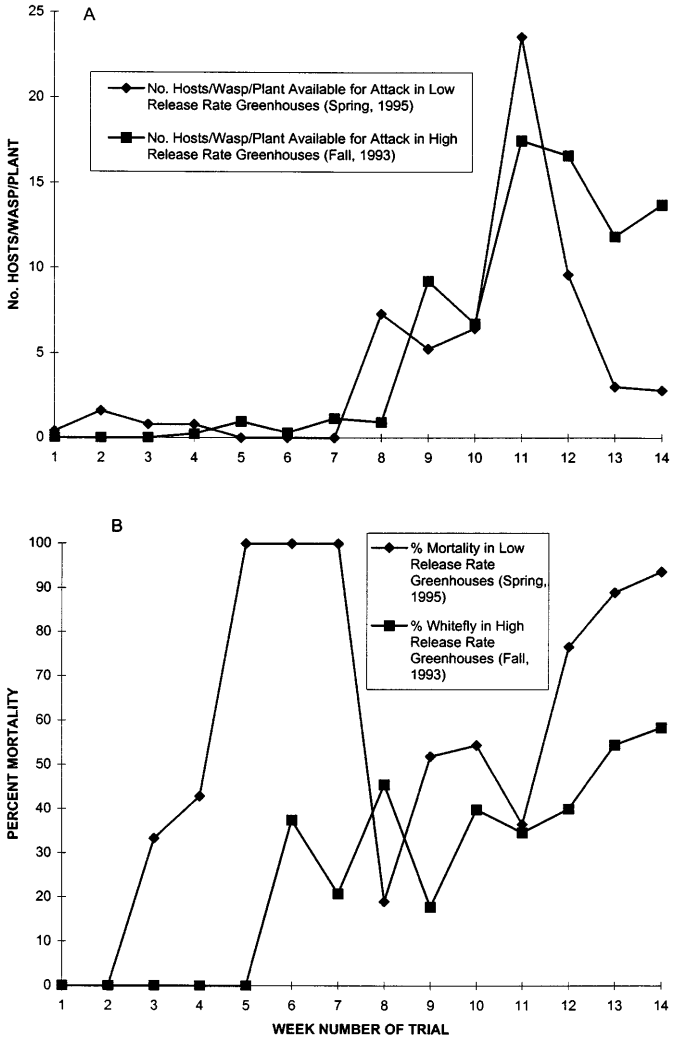

FIG. 4. The average number of susceptible *Bemisia argentifolii* nymphs and pupae per plant (A) available for host feeding and parasitism by individual wasps (*Encarsia formosa*) for the low and high release rate greenhouses, and (B) the percentage mortality of *Bemisia argentifolii* nymphs and pupae in the presence of *Encarsia formosa* averaged in the low and high release rate greenhouses.

Massachusetts.) The mean number of nymphs per leaf did not differ significantly between parasitoid release treatments or plants treated with insecticides ($F = 1.47$, $df = 1032$, $P = 0.23$). Immature whiteflies in the high release rate greenhouses were found on a larger percentage of plants (70%) than insecticide treated plants (30%) (Table 8). This indicates that the high release rate of *E. formosa* produced a poinsettia crop with similar final numbers of live immature whiteflies, but survivors were spread over a larger number of plants. Fewer plants in the low release greenhouses were infested when compared to percentage infested plants in the high release rate greenhouses and retail outlets (Table 8).

DISCUSSION

In small experimental greenhouses at Cornell University, life-table analyses showed that *E. formosa* released at 1 wasp/plant/week (low release rate) and 3 wasps/plant/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. 2). There was substantial reduction in net reproductive rates of *B. argentifolii* in greenhouses (88.3% reduction in high release rate greenhouses and 94.1% in low release rate greenhouses) into which *E. formosa* was released when compared to greenhouses which did not receive the parasitoid (Table 7).

Enkegaard (1993b) reports that in the laboratory at temperatures spanning the average temperature range in the low and high release rate greenhouses, and when *B. argentifolii* is the host on poinsettia, *E. formosa* should be able to control *B. argentifolii* because the parasitoid's developmental time is shorter, and its net reproductive rate (R_0) and intrinsic rate of increase (r_m) are greater than those of *B. argentifolii*. Our results have shown that the high release rate of *E. formosa* gave control comparable to insecticides before imidacloprid was available in Massachusetts, and that the low release rate gave better whitefly control than the high release rate (Fig. 2B, Table 5), and the mean number of live nymphs and pupae were lower than insecticide-treated plants, although this difference was not significant (Table 8). Life-table data indicate the low release rate gave better control because net reproduction (R_0) by females from all cohorts was lower than the high release rate greenhouses (Table 7).

R_0 values for cohorts 1 + 2 in low ($R_0 = 6.25$ [Table 7]) and high ($R_0 = 9.82$ [Table 7]) release rate green-

TABLE 8

Infestation Statistics for Live *Bemisia argentifolii* Nymphs and Pupae on Poinsettia Leaves from Experimental Greenhouses in Which *Encarsia formosa* Had Been Released and on Poinsettia Leaves at Retail Outlets at the End of the Growing Season

Treatment	No. plants inspected	% Plants infested	No. leaves examined	% Leaves infested	Nymphs/leaf (±SE)
Low release rate greenhouses	30	23	180	3.9	0.09 ± 0.04
High release rate greenhouses	30	70	180	16.5	0.82 ± 0.29
Five retail outlets in Amherst, MA	112	30	672	8.8	0.69 ± 0.20

houses were greater than one indicating population growth for these cohorts (Table 7) (Carey 1993). Females from cohorts 1 + 2 would have an expected longevity of approximately 22 days at 21–25°C (average temperature range in the experimental greenhouses) and lifetime fecundity of approximately 44 eggs (Enkegaard, 1990, 1993a). Egg-laying over the course of the female's lifetime would result in overlapping lifestages. Consequently, progeny would not be simultaneously available for attack by *E. formosa* and would be appearing over the 3-week oviposition period, and whitefly population decline because of parasitoid action would not be observed immediately.

R_0 values for cohort 3 (the last cohort that would have the opportunity to reproduce on poinsettia before harvest) were less than one in both trials (Table 7), indicating that population density should decline. Declining population densities were observed after week 11 in the low release rate greenhouses (Fig. 2B) and after week 12 in the high release rate greenhouses (Fig. 2B) as progeny produced by females from cohorts 1 + 2 were killed by parasitoids.

The decline in population growth took longer to occur and was smaller in the high release rate greenhouses (Fig. 2B) because more progeny were born into these greenhouses over the 22-day life expectancy of females from cohorts 1 + 2 when compared to the low release rate greenhouses where R_0 for cohorts 1 + 2 was 1.6× lower (Table 7). The reason *E. formosa* killed fewer whiteflies in the high release rate greenhouses may be attributable to mutual interference between searching parasitoids.

Mutual interference results from interactions between natural enemies, which reduces searching efficiency (Hassell and Varley, 1969; Hassell, 1971). Three forms of mutual interference are recognized (Visser and Driessen, 1991): (1) Direct mutual interference: conspecifics disrupt search through direct physical contact (Hassell and Varley, 1969; Hassell, 1971). (2) Indirect mutual interference: superparasitism by conspecifics reduces the numbers of hosts killed per female per patch (Visser and Driessen, 1991). (3) Pseudo-interference: is the non-random distribution of parasitoids among host patches resulting in differential patch exploitation. Searching efficiency decreases as parasitoid densities increase (Free *et al.*, 1977).

Encarsia formosa exhibits oriented flight to host plants infested with *T. vaporariorum* (Guerrieri, 1997) and is arrested on infested leaves by encounters with honeydew, unparasitized and parasitized whitefly nymphs, which increases residence time (van Vianen and van de Viere, 1988; van Roermund *et al.*, 1994; van Roermund and van Lenteren, 1995). Together, these observations may explain congregations of parasitoids on whitefly-infested tomato plants in greenhouses (Hussey *et al.*, 1976; Ledieu, 1976) thereby creating conditions in which mutual interference could occur. In our study, mutual interference (the type is undetermined) would be expected to be greatest at the high release rate when plants are small (cohorts 1 + 2) because wasps would not be diluted over a large plant canopy, and the likelihood of searching females encountering conspecifics or utilized hosts in patches would be higher. Lower levels of mortality were observed in high release rate greenhouses (74% mortality, Table 4) when compared to the low release rate greenhouses (80% mortality, Table 2) for cohorts 1 + 2. Yano (1987) reports that as the number of *E. formosa* searching for *T. vaporariorum* on greenhouse tomatoes increased, the number of nymphs killed by individual females decreased.

Mutual interference may account for the varying levels of *B. argentifolii* control on poinsettia when different release rates of *E. formosa* are used. When two or fewer *E. formosa* are released per poinsettia per week, adequate control of *B. argentifolii* is achieved (Ronchi *et al.*, 1994; Stenseth, 1993). When the release rate is three wasps or more per plant per week, inadequate control of *B. argentifolii* results (Parrella *et al.*, 1991; Hoddle and Van Driesche, 1996). The results of the trials presented here, and those of Hoddle and Van Driesche (1996), both support the suggestion that as weekly release rates of *E. formosa* increase, overall *B. argentifolii* mortality decreases, and percentage parasitism increases (Fig. 5). Increase in percentage parasitism may result because patch abandonment due to mutual interference occurs before over-exploitation (superparasitism and host feeding of parasitized whitefly nymphs prior to parasitoid egg hatch) is realized,

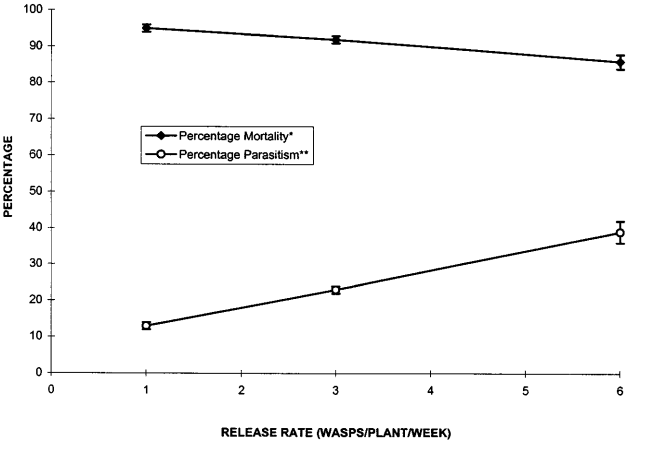

FIG. 5. Total percentage mortality and parasitism trends (±SD of the sample proportion) for *Bemisia argentifolii* on poinsettia in the presence of three different weekly release rates of *Encarsia formosa* (data from Table 5 and Hoddle and Van Driesche, 1996). * % Mortality is death from all causes combined, i.e., parasitism, host feeding, aborted parasitism, and naturally occurring mortality in wasp release greenhouses. ** % Parasitism is the proportion of immature whiteflies with developing parasitoids.

thus greater numbers of hosts that were successively parasitized are conserved.

Parrella *et al.* (1991) cite mutual interference as a possible constraint on using *E. formosa* inundatively for *B. argentifolii* control, particularly when poinsettias are small. Further behavioral studies on *E. formosa* are needed to determine how multiple females interact and behave on whitefly patches, and if a form of mutual interference is responsible for declining parasitoid efficacy as weekly release rates increase.

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