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.

**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.
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 × 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 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 [metalaxy] 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**

*E. 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). *E. formosa* pupae were supplied by Bunting Biological North America (Oxnard, CA), and were shipped as parasitized *T. vaporarium* 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 subcohorts 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 macro lens, 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 fate 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 to produce life-tables for each whitefly cohort in the same greenhouse. Summary life-tables for each treatment were constructed from summary life-tables for each treatment. 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, r² = 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 (LxMx) estimates (where Lx is the fraction of females that survive to age x, and Mx 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, r² = 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 (R₀) is the per capita average number of female offspring born to a cohort of females during their lifetime, and describes the growth rate of 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 (mᵦd) was calculated from observed mortality as:

\[ mᵦd = dᵦd/(1 - mᵦ) \]

where dᵦd is Death from Unknown Causes observed with photographic sampling, and mᵦ 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:

\[ mᵢ = 1 - (1 - dᵢ)/(1 - dᵦ) \]

where mᵢ is the marginal probability of mortality from the ith cause, dᵢ is death rate from the ith cause, and dᵦ 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 (R₀)

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, r² = 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 (LₓMₓ) estimates (where Lₓ is the fraction of females that survive to age x, and Mₓ 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, r² = 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 (R₀) 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 fecun-
dity estimates were calculated as described above, and
$R_0$ were calculated by dividing the theoretical fecun-
dity 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 argensfollii 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 thereaf-

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. argensfollii live for ap-
proximately 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; Enke-
gaard, 1993b). The number of susceptible hosts per plant
available for attack by wasps (averaged for each treat-
ment, 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 calcu-
lated 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. argensfollii 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. argensfollii 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 (±SE) per leaf were 0.03 ± 0.02
and 0.03 ± 0.02, respectively, for the low and high
release rate trials ($t_{value} = 0.22$, df = 1040, $P = 0.83$).
Mean numbers of nymphs per leaf (±SE) was 0.01 ±
0.01 and 0.00 ± 0.00, respectively, for the low and high

Para
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 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.

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### TABLE 1

<table>
<thead>
<tr>
<th>Stage</th>
<th>$I_x$</th>
<th>$I_d$</th>
<th>$I_{dx}$</th>
<th>No. deaths by factor</th>
<th>Marginal probability of mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$C_{x1}$</td>
<td>$C_x$</td>
<td>$C_{x1}$</td>
<td>$C_x$</td>
<td>$C_{x1}$</td>
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<tr>
<td>Egg/crawler</td>
<td>198</td>
<td>335</td>
<td>535</td>
<td>86</td>
<td>18</td>
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<tr>
<td>Settled $I_1$</td>
<td>112</td>
<td>317</td>
<td>522</td>
<td>17</td>
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<tr>
<td>$I_2$</td>
<td>95</td>
<td>304</td>
<td>516</td>
<td>1</td>
<td>1</td>
</tr>
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<td>$I_3$</td>
<td>94</td>
<td>303</td>
<td>508</td>
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<td>3</td>
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<td>300</td>
<td>494</td>
<td>1</td>
<td>2</td>
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<tr>
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<td>91</td>
<td>298</td>
<td>480</td>
<td>0</td>
<td>1</td>
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<tr>
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<td>297$^b$</td>
<td>473$^c$</td>
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</table>

$^1$ $I_x$, 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.

<table>
<thead>
<tr>
<th>Stage</th>
<th>$I_x$</th>
<th>$I_d$</th>
<th>$I_{dx}$</th>
<th>No. deaths by factor</th>
<th>Marginal probability of mortality</th>
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<td>$C_x$</td>
<td>$C_{x1}$</td>
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<td>$C_{x1}$</td>
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<td>Egg/crawler</td>
<td>365</td>
<td>469</td>
<td>638</td>
<td>61</td>
<td>47</td>
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<tr>
<td>Settled $I_1$</td>
<td>304</td>
<td>422</td>
<td>556</td>
<td>13</td>
<td>91</td>
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<tr>
<td>$I_2$</td>
<td>291</td>
<td>331</td>
<td>383</td>
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<td>100</td>
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<td>258</td>
<td>231</td>
<td>208</td>
<td>22</td>
<td>103</td>
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<tr>
<td>$I_4$</td>
<td>236</td>
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<td>112</td>
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<tr>
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<td>1</td>
<td>27</td>
<td>4</td>
</tr>
<tr>
<td>Adults</td>
<td>73$^b$</td>
<td>0$^c$</td>
<td>0$^d$</td>
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</tbody>
</table>

$^a$ Parasite fate after parasitism was recorded photographically; see Table 6. $^b$, $^c$, $^d$ Egg to adult survivorship for B. argentifolii: $^a$ 46%, $^b$ 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%.
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 in the low release greenhouses.

### 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)

<table>
<thead>
<tr>
<th>Stage</th>
<th>$I_x$</th>
<th>$d_x$</th>
<th>$f_{dx}$</th>
<th>No. deaths</th>
<th>Marginal probability of mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$C_{1-2}$</td>
<td>$C_3$</td>
<td>$C_4$</td>
<td>$C_{1-2}$</td>
<td>$C_3$</td>
</tr>
<tr>
<td>Egg/crawler</td>
<td>295</td>
<td>593</td>
<td>841</td>
<td>63</td>
<td>85</td>
</tr>
<tr>
<td>Settled I₁</td>
<td>232</td>
<td>508</td>
<td>742</td>
<td>8</td>
<td>15</td>
</tr>
<tr>
<td>I₂</td>
<td>224</td>
<td>493</td>
<td>728</td>
<td>15</td>
<td>7</td>
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<tr>
<td>I₃</td>
<td>209</td>
<td>486</td>
<td>714</td>
<td>5</td>
<td>23</td>
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<tr>
<td>I₄</td>
<td>204</td>
<td>463</td>
<td>701</td>
<td>13</td>
<td>36</td>
</tr>
<tr>
<td>Pupae</td>
<td>191</td>
<td>427</td>
<td>686</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>Adults</td>
<td>189$^a$</td>
<td>418$^b$</td>
<td>683$^c$</td>
<td>2</td>
<td>9</td>
</tr>
</tbody>
</table>

$^a,b,c$ 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%.

### 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)

<table>
<thead>
<tr>
<th>Stage</th>
<th>$I_x$</th>
<th>$d_x$</th>
<th>$f_{dx}$</th>
<th>No. deaths</th>
<th>Marginal probability of mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$C_{1-2}$</td>
<td>$C_3$</td>
<td>$C_4$</td>
<td>$C_{1-2}$</td>
<td>$C_3$</td>
</tr>
<tr>
<td>Egg/crawler</td>
<td>254</td>
<td>450</td>
<td>878</td>
<td>44</td>
<td>103</td>
</tr>
<tr>
<td>Settled I₁</td>
<td>210</td>
<td>347</td>
<td>755</td>
<td>4</td>
<td>59</td>
</tr>
<tr>
<td>I₂</td>
<td>206</td>
<td>288</td>
<td>624</td>
<td>18</td>
<td>107</td>
</tr>
<tr>
<td>I₃</td>
<td>188</td>
<td>181</td>
<td>449</td>
<td>23</td>
<td>59</td>
</tr>
<tr>
<td>I₄</td>
<td>165</td>
<td>122</td>
<td>335</td>
<td>79</td>
<td>113</td>
</tr>
<tr>
<td>Pupae</td>
<td>86</td>
<td>9</td>
<td>56</td>
<td>20</td>
<td>7</td>
</tr>
<tr>
<td>Adults</td>
<td>66$^b$</td>
<td>2$^c$</td>
<td>56$^d$</td>
<td>20</td>
<td>5</td>
</tr>
</tbody>
</table>

$^a$ 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%.

171LIFE-TABLES OF *Bemisia argentifolii*
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 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* of Three E. formosa per Plant per Week

<table>
<thead>
<tr>
<th>Stage</th>
<th>$I_x$</th>
<th>$d_x$</th>
<th>$f_{dx}$</th>
<th>No. deaths by factor</th>
<th>Marginal probability of mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$C_1$</td>
<td>$C_3$</td>
<td>$R_1$</td>
<td>$R_3$</td>
<td>$C_1$</td>
</tr>
<tr>
<td>Egg/crawler</td>
<td>1068</td>
<td>1729</td>
<td>1472</td>
<td>1582</td>
<td>117</td>
</tr>
<tr>
<td>Settled I&lt;sub&gt;1&lt;/sub&gt;</td>
<td>951</td>
<td>1482</td>
<td>1282</td>
<td>1312</td>
<td>36</td>
</tr>
<tr>
<td>I&lt;sub&gt;2&lt;/sub&gt;</td>
<td>915</td>
<td>1445</td>
<td>1005</td>
<td>1118</td>
<td>10</td>
</tr>
<tr>
<td>I&lt;sub&gt;3&lt;/sub&gt;</td>
<td>905</td>
<td>1409</td>
<td>697</td>
<td>818</td>
<td>19</td>
</tr>
<tr>
<td>I&lt;sub&gt;4&lt;/sub&gt;</td>
<td>886</td>
<td>1368</td>
<td>476</td>
<td>622</td>
<td>17</td>
</tr>
<tr>
<td>Pupae</td>
<td>869</td>
<td>1304</td>
<td>105</td>
<td>151</td>
<td>8</td>
</tr>
<tr>
<td>Adults</td>
<td>861&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1290&lt;sup&gt;d&lt;/sup&gt;</td>
<td>73&lt;sup&gt;e&lt;/sup&gt;</td>
<td>124&lt;sup&gt;f&lt;/sup&gt;</td>
<td></td>
</tr>
</tbody>
</table>

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.

<sup>a</sup>% Parasitism (total no. parasitized in all cohorts/no. settled I<sub>1</sub> in all cohorts):<sup>a</sup> 13%, <sup>b</sup> 23%.

<sup>c</sup>-<sup>f</sup>Egg to adult survivorship for *B. argentifolii* across all cohorts: <sup>c</sup> 81%, <sup>d</sup> 75%, <sup>e</sup> 5%, <sup>f</sup> 8%.

### TABLE 6

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

<table>
<thead>
<tr>
<th>Wasp release rate</th>
<th>Cohort</th>
<th>% Emerged&lt;sup&gt;a&lt;/sup&gt;</th>
<th>% Undetermined&lt;sup&gt;b&lt;/sup&gt;</th>
<th>% Disappeared&lt;sup&gt;c&lt;/sup&gt;</th>
<th>% Died&lt;sup&gt;d&lt;/sup&gt;</th>
<th>% Parasitism&lt;sup&gt;e&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Wasp/plant/week (Low release rate trial)</td>
<td>1 + 2</td>
<td>60</td>
<td>27</td>
<td>1</td>
<td>12</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>45</td>
<td>47</td>
<td>0</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>45</td>
<td>48</td>
<td>3</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Average % parasitism&lt;sup&gt;f&lt;/sup&gt;: 13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 Wasps/plant/week (High release rate trial)</td>
<td>1 + 2</td>
<td>57</td>
<td>22</td>
<td>0</td>
<td>22</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>79</td>
<td>13</td>
<td>2</td>
<td>6</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>24</td>
<td>67</td>
<td>2</td>
<td>7</td>
<td>29</td>
</tr>
<tr>
<td>Average % parasitism: 23</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Emergence of parasitoid recorded photographically.

<sup>b</sup> Photography of parasitized whitefly ceased before developmental outcome was determined.

<sup>c</sup> Parasitized whitefly disappeared before developmental fate was determined.

<sup>d</sup> Parasite died inside host.

<sup>e</sup>% Parasitized was calculated as total no. nymphs parasitized across both replicates/total no. of settled first instars in that particular cohort across both replicates.

<sup>f</sup>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 $57\times$ 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 $16\times$ 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 $= \frac{d_i}{I_0}$, where $d_i$ is death in the $i$th stage, and $I_0$ 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).

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 greenhouse 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-
The 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 0.08% that of the corresponding 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% 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.

At week 14, the average number of hosts available for attack per wasp per plant was 4.7 ± 0.3 higher in the high release rate greenhouses, and percentage mortality was 1.6 ± 0.3 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...
The mean number of nymphs per leaf did not differ significantly between parasitoid release treatments or plants treated with insecticides ($F_{5,1032} = 1.47, P = 0.23$). 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

<table>
<thead>
<tr>
<th>Treatment</th>
<th>No. plants inspected</th>
<th>% Plants infested</th>
<th>No. leaves examined</th>
<th>% Leaves infested</th>
<th>Nymphs/leaf ($±SE$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low release rate greenhouses</td>
<td>30</td>
<td>23</td>
<td>180</td>
<td>3.9</td>
<td>0.09 ± 0.04</td>
</tr>
<tr>
<td>High release rate greenhouses</td>
<td>30</td>
<td>70</td>
<td>180</td>
<td>16.5</td>
<td>0.82 ± 0.29</td>
</tr>
<tr>
<td>Five retail outlets in Amherst, MA</td>
<td>112</td>
<td>30</td>
<td>672</td>
<td>8.8</td>
<td>0.69 ± 0.20</td>
</tr>
</tbody>
</table>
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 with developing parasitoids (superparasitism and host feeding of parasitized whitefly nymphs prior to parasitoid egg hatch) is realized, with lesser numbers of hosts killed per female 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.

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, adequate 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.


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.

** % Parasitism is the proportion 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.

Parrèlla et al. (1991) cite mutual interference as a possible constraint on using E. formosa inadu-tantly 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 effi-

cacy as weekly release rates increase.

ACKNOWLEDGMENTS

We thank K. C. Bennett for technical assistance at Cornell University. Paul Ecke Ranch, Encinitas, California, donated the cuttings used in evaluation trials. The help of Dr. R. Greetrex (CIBA-Bunting, England) and D. Cahn of Bunting Biological North America (Oxnard, CA), is gratefully acknowledged. This research was supported by grants from the Massachusetts IPM program, USDA/NRI/CP Grant No. 9402481, and CIBA-Bunting.

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