Biological Control of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on Poinsettia with Inundative Releases of *Encarsia formosa* Beltsville Strain (Hymenoptera: Aphelinidae): Can Parasitoid Reproduction Augment Inundative Releases?

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ABSTRACT The effectiveness of inundative releases of the parasitoid *Encarsia formosa* Beltsville strain for control of *Bemisia argentifolii* Bellows & Perring on poinsettia (*Euphorbia pulcherrima* Willd. ex Koltz.) was determined in replicated experimental greenhouses. We evaluated 2 release rates of *E. formosa* Beltsville strain: a low release rate (1 wasp per plant per week, released in 2 greenhouses) and a high release rate (3 wasps per plant per week, released in 2 greenhouses), over a 14-wk growing season. The trial had 1 control greenhouse in which *B. argentifolii* developed on poinsettia in the absence of *E. formosa* Beltsville strain. Life-tables were constructed for *B. argentifolii* in the presence and absence of *E. formosa* Beltsville strain 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* Beltsville strain, egg to adult survivorship of *B. argentifolii* on poinsettia was 71%. At the low release rate, egg to survivorship of *B. argentifolii* was 4% and parasitism was 23%. At the high release rate, egg to adult survivorship for *B. argentifolii* was 1% and parasitism was 12%. The net reproductive rates (R_o) for *B. argentifolii* populations in the absence of *E. formosa* Beltsville strain was 17.1, indicating a rapidly increasing population. Net reproductive rates for whitefly populations subject to wasp releases were 0.95 for the low release rate greenhouses, and 0.32 for the high release rate greenhouses, indicating declining *B. argentifolii* population growth. The high release rate provided better control of *B. argentifolii* than the low release rate and this was attributed to higher levels of in-house wasp reproduction. At time of harvest, the mean number of live nymphs and pupae per leaf in the high release rate greenhouses was not significantly different from numbers counted on leaves on plants being sold at commercial retail outlets.

KEY WORDS *Bemisia argentifolii*, whitefly, *Encarsia formosa* Beltsville strain, parasitoid, poinsettia, greenhouse

BIOLOGICAL CONTROL OF insect pests attacking ornamental plants (cut flowers, potted foliage, and flowering plants) grown in greenhouses is not commonly practiced (Parrella et al. 1991), even though >32,000 ha of greenhouse production throughout the world are devoted to ornamentals (Parrella 1990). Several reasons exist for why biological control in ornamental crops is still in its infancy. First, extreme standards for aesthetic quality at time of sale demand minimal pest damage (Parrella 1990, Parrella et al. 1991). Second, pest control costs are low, ≈1% of production costs in greenhouses (van Lenteren and Woets 1988). Consequently, cost has not constrained pesticide use. Third, strict quarantine requirements for exports has promoted intensive use of pesticides to eradicate arthropod contaminants (Parrella 1990). Fourth, lack of rigorous research documenting the success of biological control at various natural enemy release rates and lack of economic analyses of biological control in greenhouses have hindered practical application (Parrella et al. 1992).

Poinsettia, *Euphorbia pulcherrima* Willd. ex Koltz., a greenhouse grown ornamental, is the number one potted crop grown in the United States with >40 million plants produced per year (Parrella et al. 1991). The major phytophagous pest attacking this crop in the United States is the whitefly, *Bemisia argentifolii* Bellows & Perring (Homoptera: Aleyrodidae) [=*B. tabaci* (Gennadius) strain B (Bellows et al. 1994, Heinz and Parrella 1994, Hoddle and Van Driesche 1996)].

Whitefly damage to commercial poinsettia production is primarily a reduction in aesthetic quality

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that leads to reduced marketability. Growers have very low tolerances for whitefly nymphs, adults, and honeydew in poinsettia crops (Hoddle and Van Driesche 1996), and use regular insecticide applications to ensure that whitefly populations do not develop to levels able to reduce plant vigor, foliage production, or bract quality (Heinz and Parrella 1994).

Bemisia argentifolii is particularly prone to develop resistance to insecticides; and resistance by this species to organophosphates, carbamates, and pyrethroids has been documented (Costa and Brown 1991, Cahill et al. 1995). Currently in the United States, *B. argentifolii* is controlled effectively on poinsettia with imidacloprid, a systemic chloronicotinyl insecticide that gives 10–12 wk whitefly control with a single application (Lopes 1994). This compound was registered for greenhouse use in the United States in 1994 (Sanderson and Roush 1995). In Spain, imidacloprid is used for whitefly control on outdoor vegetable crops and resistance was observed after 3 yr of use (Sanderson and Roush 1995, Cahill et al. 1996). Once a whitefly population on poinsettia develops resistance to imidacloprid in the United States, it will rapidly become widespread within a very short period because of the extensive exchange of plants and cuttings (Parrella 1995).

Incorporation of natural enemies into an integrated pest management (IPM) program for *B. argentifolii* on poinsettia would diversify whitefly control options, reduce reliance on insecticides, and provide a more sustainable whitefly control system for the crop. A potentially effective natural enemy that has been identified from laboratory work for inundative control of *B. argentifolii* on poinsettia in greenhouses is a strain of *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) from Beltsville, MD (Heinz and Parrella 1994, van Lenteren and Brasch 1994).

The Beltsville strain of *E. formosa* was developed from wasps initially found attacking the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), but subsequently reared on *B. argentifolii* with poinsettia as the host plant at USDA–ARS laboratory Beltsville, MD (Bentz 1993, Heinz and Parrella 1994).

In the laboratory, *E. formosa* Beltsville strain had the highest parasitization rates, lowest levels of host feeding, highest total kill of whitefly nymphs, highest progeny survivorship, and high longevity when compared with 4 other *Encarsia* spp. attacking *B. argentifolii* on poinsettia (Heinz and Parrella 1994). Heinz and Parrella (1994) proposed that *E. formosa* Beltsville strain might be better adapted to *B. argentifolii* than the other parasitoids tested.

Better performance by *B. argentifolii*-reared *E. formosa* may be a genetic response to selection or environmental conditioning (Henter et al. 1993, Henter and van Lenteren 1996, Henter et al. 1996). *B. argentifolii* adapted strains of *E. formosa* also readily parasitize *T. vaporariorum* (van Lenteren and Brasch 1994) and this may simplify biological control of both whiteflies when they occur together.

As part of an IPM project to prevent resistance development and improve *B. argentifolii* management on poinsettia in Massachusetts, we have been evaluating the suitability of various parasitic wasps for the biological control of *B. argentifolii*. One of our candidate parasitoids for potential use in the IPM program was *E. formosa* Beltsville strain. Evaluations of *E. formosa* reared on *T. vaporariorum*, and *Eretmocerus eremicus* Rose and Zolnerowich for *B. argentifolii* control on poinsettia have already been reported, based on studies in experimental greenhouses (Hoddle et al. 1996a, b).

In the study reported here, we tested a low (1 wasp per plant per week) and high (3 wasps per plant per week) release rate of *E. formosa* Beltsville strain for control of *B. argentifolii* on poinsettia. We used replicated experimental greenhouses and a photographic technique to construct paired life-tables for *B. argentifolii* on poinsettia in the presence and absence of *E. formosa* Beltsville strain. In addition to life-table construction, we made weekly population counts of the numbers of immature and adult *B. argentifolii* and parasitized whitefly nymphs on the poinsettia plants in the experimental greenhouses.

Our objectives were to use life-tables and population counts to determine over the course of a 14-wk poinsettia crop: how well *E. formosa* Beltsville strain suppressed *B. argentifolii* population growth compared with the whitefly population growth of a control population, if our low and high release rates of *E. formosa* Beltsville strain differed in the level of control given, and the mechanisms by which the parasitoid releases affected whitefly population growth.

Materials and Methods

Experimental Greenhouses, Crop Management, and Initial Whitefly Infestation Levels. Evaluations of *E. formosa* Beltsville strain were conducted in small, identical plastic greenhouses at Cornell University, Ithaca, NY. Each greenhouse (5 by 4 by 3.5 m) held 6 benches (0.91 by 1.5 by 0.91 m), each with 15 pots (15 cm diameter, with single stem poinsettias), for a total of 90 plants per greenhouse. The trial was run in the fall of 1994 and included 5 greenhouses; 1 control greenhouse (no wasps released), 2 low release rate greenhouses (1 wasp per plant per week), and 2 high release rate greenhouses (3 wasps per plant per week). Four DDVP (Roxide Int., NY) fumigant strips were hung in the control greenhouse to prevent parasitoid establishment. DDVP is used to keep our whitefly colony parasitoid free with no adverse effects on whitefly population growth. The poinsettia cultivar used was 'Freedom Red', and the trial ran for 14 wk.

The poinsettia crop was 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 200ppm, Peter's S.T.E.M 0.01 g/liter (Grace-Sierra Hort. Prod., CA), and ammonium molybdate liquid concentrate (Mallinckrodt, KY) at 0.17 ml/liter applied at every watering), root rot control (Subdue [metalaxyl] [Ciba-Geigy Corp., NC] soil drench hand poured at weeks 2 and 11 of each trial at a rate of 0.15 g/liter), fungus gnat control (Gnatrol [*Bacillus thuringiensis* subsp. *israelensis*] [Abbott Lab., IL] applied at weeks 3, 5, and 7 at a rate of 2.66 ml/liter), and pinching (3 wk after potting). Maximum and minimum temperatures were recorded daily.

Estimates of initial *B. argentifolii* densities on poinsettia cuttings from the supplier were made before potting by recording the number of live nymphs, pupae and adults on each leaf of 102 randomly chosen cuttings.

Parasitoid Release Regimen. *E. formosa* Beltsville strain was evaluated at 2 release rates. The low release rate was 1 female per plant per week, and the high release rate was 3 females per plant per week. The trial was conducted in the fall of 1994 (8 September to 14 December 1994 inclusive). *E. formosa* Beltsville pupae were supplied by American Insectaries, Escondido, CA, and were shipped as loose parasitized *B. argentifolii* nymphs in petri dishes. The host plant used for *E. formosa* Beltsville strain mass rearing on *B. argentifolii* was cabbage, *Brassica oleracea capitata*. After receipt, wasps were allowed to emerge into petri dishes on the lids of which were thin streaks of honey. Before 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 within greenhouses, and opened below the plant canopy. 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 (3–88 whitefly nymphs per cohort) 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* Beltsville strain (after Summy et al. 1984, Gould et al. 1992, and Hoddle et al. 1996a–c).

To establish a cohort of whiteflies, 10–13 poinsettia plants randomly selected from each greenhouse were taken to the laboratory and clip cages were placed on 1 leaf of each plant. In each cage, 1–4 mating pairs of whiteflies were introduced and left to oviposit for 2–3 d at 25°C. Cages and whiteflies were then removed, the number of eggs recorded, and plants returned to their original location within 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 pooled over the set of all plants returned to each greenhouse were standardized between greenhouses by removing eggs from subcohorts with a 000 size insect pin. This ensured that equal numbers of new whiteflies (in cohorts) were added to each greenhouse. Subcohorts were set up for photography at weeks 1 and 2 (designated whitefly cohorts 1 and 2), 5 (cohort 3) and 9 (cohort 4) of the trial. These cohorts thus occurred during, approximately, the 1st, 2nd, and 3rd whitefly generations, respectively. Eight to 10 d after whiteflies were removed from clip cages, the numbers of 1st instar nymphs that had emerged and settled from the counted eggs were recorded. Area of leaf (35 by 23 mm) on which most nymphs had settled was photographed. Photography commenced immediately after the nymphs in each subcohort had settled. Each subcohort was photographed twice on each examination date (an insurance measure for unfocused slides), and photography was repeated 2 times each week. Photography of a subcohort ceased when all the nymphs or pupae had died, disappeared, emerged as adult whiteflies, or produced adult parasitoids.

The camera used was a 35-mm single lens reflex outfitted with a 55-mm macrolense, a dedicated ringflash, and 1 extension tube. F-stop and aperture settings were 16 and 22, respectively. The film used was 50 asa color slide film.

Slides of each subcohort 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 1st instars that were observed in the 1st photograph of each subcohort was calculated as the ratio of the number of nymphs photographed to the number on the leaf as a whole, multiplied by the total number of eggs laid on the leaf (see Hoddle et al. 1996c 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 subcohorts 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*, di-

vided 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). Because 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

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

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 3 contemporaneous factors were calculated as

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

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

Sex Ratio of Emerging Whiteflies, Net Fecundity Estimates, and Calculation of Net Reproductive Rates (R_o). Sex ratio (females/males + females) for *B. argentifolii* on poinsettia is correlated positively 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 1990, 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 that 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 5 controlled temperatures (16–28°C). Net fecundity is correlated positively with temperature, and is described by $NF = 6.3474T\text{-}102.11$, $r^2 = 0.968$, 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_o) 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_o 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 $R_o < 1$ indicate a declining population, $R_o > 1$ an increasing population, and $R_o = 1$ a stable population (Carey 1993).

Monitoring *B. argentifolii* Population Densities. Population counts of immature and adult whiteflies on poinsettia leaves were made weekly. Numbers of 1st and 2nd, 3rd, 4th-instar nymphs, pupae, exuviae from which either adult whiteflies or parasitoids had emerged, and adult whiteflies were recorded.

Over the course of the trial, plants were divided by height into 3 strata, and all immature whiteflies were counted on a fixed number of tagged leaves within each stratum. Stratum 1 consisted of the leaves originally present on the newly potted cuttings. For stratum 1, one leaf on each of 15 randomly selected plants was tagged in each greenhouse and inspected weekly. After 5–6 wk of plant growth, 1 leaf in the top portion of an additional 15 randomly selected plants was tagged in each greenhouse. These leaves were designated stratum 2, and whitefly counts were made in both strata 1 and 2 each week thereafter. After an additional 4–5 wk of growth (around week 10–11 of the trial), another 15 plants in each greenhouse had 1 leaf tagged at the top of the plant and inspected weekly. This upper most leaf layer was designated stratum 3. At this time, 15 leaves were being examined weekly in each of three strata for a total of 45 leaves, 1 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 by way of in-house reproduction was calculated from the weekly estimates of numbers of whitefly nymphs 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. Because whitefly nymphs with parasitoid exit holes accumulated on leaves, each weekly estimate had the count from the preceding week subtracted to give net estimates of wasps emerging into the

Table 1. Life-table for *B. argentifolii* in the absence of *E. formosa* Beltsville strain

Stage	l_x			d_x			f_{dx}	No. deaths by factor			Marginal probability of mortality		
	C_{1-2}	C_3	C_4	C_{1-2}	C_3	C_4		C_{1-2}	C_3	C_4	C_{1-2}	C_3	C_4
Egg/Crawler	213	531	851	44	115	180	Unknown death	44	115	180	0.21	0.22	0.21
Settled 1st instar	169	416	671	4	8	32	Unknown death	3	2	4	0.02	0.005	0.01
							Disappearance	1	6	28	0.01	0.01	0.04
2nd instar	165	408	639	9	6	16	Unknown death	7	5	9	0.04	0.01	0.01
							Disappearance	2	1	7	0.01	0.002	0.01
3rd instar	156	402	623	4	8	9	Unknown death	4	5	5	0.03	0.01	0.01
							Disappearance	0	3	4	0.00	0.01	0.01
4th instar	152	394	614	2	4	11	Unknown death	2	2	11	0.01	0.01	0.02
							Disappearance	0	2	0	0.00	0.01	0.00
Pupae	150	390	603	0	2	2	Unknown death	0	2	0	0.00	0.01	0.00
							Disappearance	0	0	2	0.00	0.00	0.003
Adults	150[a]	388[b]	601[c]										

Average egg to adult survivorship for *B. argentifolii* in the absence of *E. formosa* Beltsville strain releases was 71%.

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

[a] Egg to adult survivorship for *B. argentifolii*, 70%.

[b] Egg to adult survivorship for *B. argentifolii*, 73%.

[c] Egg to adult survivorship for *B. argentifolii*, 71%.

greenhouse. We assumed wasps, once emerged, lived for 1 wk only.

Estimating the Number of Hosts Available per Plant for Wasp Attack. *E. formosa* reared on *T. vaporariorum* will parasitize 2nd, 3rd, and 4th-instar *B. argentifolii* nymphs, and it will host feed on all immature lifestages including pupae (Boisclair et al. 1990, Enkegaard 1993b). We assumed that *E. formosa* Beltsville strain reared on *B. argentifolii* had similar preferences for oviposition and host feeding. 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 to 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 of Mortality and Percentage of Parasitism in Experimental Greenhouses. Average percentage of 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 6 leaves removed (2 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 with similarly collected data from 72 poinsettias observed at 5 retail outlets in Amherst, MA, in December 1994. Mean number of nymphs per leaf were compared using a 1-way analysis of variance and Tukey's honestly significant difference mean separation test at 0.05 level of significance. The purpose of the end of crop sales inspection was to determine the efficacy of *E. formosa* Beltsville strain for *B. argentifolii* control on poinsettias when compared with plants produced with insecticides.

Results

Estimates of Initial Whitefly Infestation on Cuttings Before Potting. Initial *B. argentifolii* infestation on each of 102 cuttings prior to potting was low. Mean ± SE numbers of eggs, nymphs, and adults per leaf were 0.10 ± 0.05, 0.13 ± 0.05, and 0.00 ± 0.00, respectively.

Life-Tables for *B. argentifolii* in the Presence and Absence of *E. formosa* Beltsville Strain. Life-tables for each whitefly cohort combined across replicated treatments are presented in Tables 1–3. A summary life-table combining data across all whitefly cohorts and replicated treatments is presented in Table 4. Survival of immature parasitoids after parasitism had been observed in photographs and percentage of parasitism data for combined whitefly cohorts in wasp release greenhouses are given in Table 5.

In the absence of parasitoids, whitefly mortality was highest in the egg/crawler stage and lowest in the pupal stage (Tables 1 and 4). In the control greenhouse, egg to adult survivorship for *B. argentifolii* was similar across successive cohorts as poinsettia plants matured and survivorship averaged 71% across all cohorts (Tables 1 and 4).

In the low release rate greenhouses, egg to adult survivorship averaged across both replicates was

Table 2. Combined life-table (2 replicates) for *B. argentifolii* which received one *E. formosa* Beltsville strain per plant per week (low release rate trial)

Stage	l_x			d_x			f_{dx}	No. deaths by factor			Marginal probability of mortality		
	C_{1-2}	C_3	C_4	C_{1-2}	C_3	C_4		C_{1-2}	C_3	C_4	C_{1-2}	C_3	C_4
Egg/Crawler	308	522	831	109	45	102	Unknown death	109	45	102	0.35	0.09	0.12
Settled 1st instar	199	477	729	29	45	240	Unknown death	20	38	212	0.10	0.08	0.30
							Disappearance	9	7	28	0.05	0.01	0.04
2nd instar	170	432	489	36	90	156	Unknown death	36	89	149	0.21	0.21	0.31
							Disappearance	0	1	7	0.00	0.002	0.01
3rd instar	134	342	333	16	57	130	Unknown death	15	56	126	0.11	0.16	0.38
							Disappearance	1	1	4	0.01	0.003	0.01
4th instar	118	285	203	66	267	202	Unknown death	10	74	118	0.12	0.54	0.96
							Disappearance	0	3	0	0.00	0.01	0.00
							Parasitized	56[a]	190[a]	84[a]	0.50	0.86	0.89
Pupae	52	18	1	4	3	0	Unknown death	4	3	0	0.08	0.17	0.00
Adults	48[b]	15[c]	1[d]										

Average egg to adult survivorship for *B. argentifolii* with the release of 1 *E. formosa* Beltsville strain per plant per week (both low release rate greenhouses combined) was 4%. See Table 1 for abbreviations.

[a] Parasite fate after parasitism was recorded photographically see Table 5.

[b] Egg to adult survivorship for *B. argentifolii*, 16%.

[c] Egg to adult survivorship for *B. argentifolii*, 3%.

[d] Egg to adult survivorship for *B. argentifolii*, 0.1%.

greatest in cohorts 1 and 2 at 16%, and declined to 3 and 0.1% in cohorts 3 and 4, respectively (Table 2). Egg to adult survivorship averaged 4% across all cohorts for both low release rate greenhouses (Tables 2 and 4). In the high release rate greenhouses, egg to adult survivorship averaged across both replicates was greatest in cohorts 1 and 2 at 5%, and it declined to 0% in cohorts 3 and 4 (Table 3). Egg to adult survivorship averaged across all cohorts for both replicates was significantly lower in the high release greenhouses at 1% (z-test for differences between population proportions) than that in the low release rate treatment ($z = 4.48$, $z_{crit(0.05)} = 1.65$) (Table 4).

The trend for marginal probability of mortality for unknown death averaged across both low release rate greenhouses increased across successive whitefly generations for instars 1–4 (Table 2). The percentage of nymphs parasitized in low release rate greenhouses was highest in cohort 3, lowest in cohort 4, and intermediate in cohorts 1 and 2 (Tables 2 and 5). In the high release rate greenhouses, the observed trend for unknown death was different. Marginal probability of mortality for unknown death increased across successive cohorts for instars 1 and 2 (Table 3). Whereas, for instars 3 and 4, marginal probability of mortality for unknown death was generally highest in cohort 3, lowest in

Table 3. Combined life-table (2 replicates) for *B. argentifolii* which received 3 *E. formosa* Beltsville strain per plant per week (high release rate trial)

Stage	l_x			d_x			f_{dx}	No. deaths by factor			Marginal probability of mortality		
	C_{1-2}	C_3	C_4	C_{1-2}	C_3	C_4		C_{1-2}	C_3	C_4	C_{1-2}	C_3	C_4
Egg/Crawler	365	470	691	74	130	114	Unknown death	74	130	114	0.20	0.28	0.16
Settled 1st instar	291	340	577	24	77	233	Unknown death	15	68	221	0.05	0.21	0.39
							Disappearance	9	9	12	0.03	0.03	0.02
2nd instar	267	263	344	62	116	182	Unknown death	59	115	180	0.22	0.44	0.53
							Disappearance	3	1	2	0.01	0.004	0.01
3rd instar	205	147	162	41	83	72	Unknown death	38	82	71	0.19	0.56	0.44
							Disappearance	3	1	1	0.01	0.01	0.01
4th instar	164	64	90	140	64	90	Unknown death	33	52	62	0.36	1.00	1.00
							Parasitized	107[a]	12[a]	28[a]	0.77	1.00	1.00
Pupae	24	0	0	4	0	0	Unknown death	4	0	0	0.17	0.00	0.00
Adults	20[b]	0[c]	0[d]										

Average egg to adult survivorship for *B. argentifolii* with the release of 3 *E. formosa* Beltsville strain per plant per week (both high release rate greenhouses combined) was 1%.

[a] Parasite fate after parasitism has been recorded photographically see Table 5.

[b] Egg to adult survivorship for *B. argentifolii*, 5%.

[c] Egg to adult survivorship for *B. argentifolii*, 0%.

[d] Egg to adult survivorship for *B. argentifolii*, 0%.

Table 4. Summary life-tables across cohorts for *B. argentifolii* in the absence (1 greenhouse) and presence of 1 *E. formosa* Beltsville strain per plant per week (2 greenhouses), and 3 *E. formosa* Beltsville strain per plant per week (2 greenhouses)

Stage	l_x			d_x			f_{dx}	No. deaths by factor			Marginal probability of mortality		
	C	R_1	R_3	*C*	R_1	R_3		*C*	R_1	R_3	*C*	R_1	R_3
Egg/Crawler	1,595	1,661	1,526	339	256	318	Unknown death	339	256	318	0.21	0.15	0.21
Settled 1st instar	1,256	1,405	1,208	44	314	334	Unknown death	9	270	304	0.01	0.20	0.26
							Disappearance	35	44	30	0.03	0.03	0.02
2nd instar	1,212	1,091	874	31	282	360	Unknown death	21	274	354	0.02	0.25	0.41
							Disappearance	10	8	6	0.01	0.01	0.01
3rd instar	1,181	809	514	21	203	196	Unknown death	14	197	191	0.01	0.25	0.38
							Disappearance	7	6	5	0.01	0.01	0.01
4th instar	1,160	606	318	17	535	294	Unknown death	15	202	147	0.01	0.56	0.73
							Disappearance	2	3	0	0.002	0.005	0.00
							Parasitized	0	330[a]	147[b]	0.00	0.73	0.73
Pupae	1,143	71	24	4	7	4	Unknown death	2	7	4	0.002	0.10	0.17
							Disappearance	2	0	0	0.002	0.00	0.00
Adults	1,139[c]	64[d]	20[e]										

C, unreplicated control greenhouse (no wasp releases). R_1, two low release rate greenhouses combined across all cohorts (1 wasp per plant per week). R_3, two high release rate greenhouses combined across all cohorts (3 wasps per plant per week). See Table 1 for abbreviations.

[a] Percentage parasitism (total no. parasitized in all cohorts/no. settled 1st instars in all cohorts), 23%.
[b] Percentage parasitism (total no. parasitized in all cohorts/no. settled 1st instars in all cohorts), 12%.
[c] Egg to adult survivorship for *B. argentifolii* across all cohorts, 71%.
[d] Egg to adult survivorship for *B. argentifolii* across all cohorts, 4%.
[e] Egg to adult survivorship for *B. argentifolii* across all cohorts, 1%.

cohorts 1 and 2, and intermediate in cohort 4 (Table 3). In the high release rate greenhouses, the percentage of nymphs parasitized was lower in cohorts 3 and 4 when compared with cohorts 1 and 2 (Tables 3 and 5). Average percentage parasitism across all cohorts and both replicated greenhouses was 1.9 times higher in the low release rate greenhouses (23%) when compared with the high release rate greenhouses (12%) (Table 5).

The smallest difference in marginal probability of mortality for unknown death between the control greenhouse and the low release rate greenhouses when compared across all cohorts and replicates was in the egg/crawler stage, where unknown death was 1.4 times lower in the low release rate greenhouses than the control greenhouse. In the high release rate greenhouses, marginal probability of mortality for unknown death for the egg/crawler stage was the same as the control greenhouse (Table 4). The largest difference in marginal probability of mortality for unknown death between the control greenhouse with the low release rate greenhouses and the high release rate greenhouses was in the 4th instar, where mortality from unknown death was 56 and 73 times higher in the low release rate and high release rate greenhouses, compared with the control greenhouse, respectively (Table 4).

Survivorship Curves. Survivorship curves (percentage entering successive lifestages) calculated

Table 5. Parasitoid fate (*E. formosa* Beltsville strain) 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	43	57	0	0	28
	3	62	31	2	5	40
	4	6	89	1	4	12
						Avg % parasitism, 23%
3 wasps/plant/week (high release rate trial)	1 + 2	58	41	0	1	37
	3	58	9	0	33	4
	4	0	86	0	14	5
						Avg % parasitism, 12%

Average percentage parasitism, total number of parasitized nymphs/total number of settled 1st instars across all cohorts and replicates (Table 4).

[a] Emergence of parasitoid recorded photographically.
[b] Photography of parasitized nymphs ceased before developmental outcome was determined.
[c] Parasitized nymphs disappeared before developmental fate was determined.
[d] Parasite died inside host.
[e] Percentage parasitized was calculated as total number of parasitized nymphs/total number of settled 1st instars for each cohort across replicates (Tables 2 and 3).

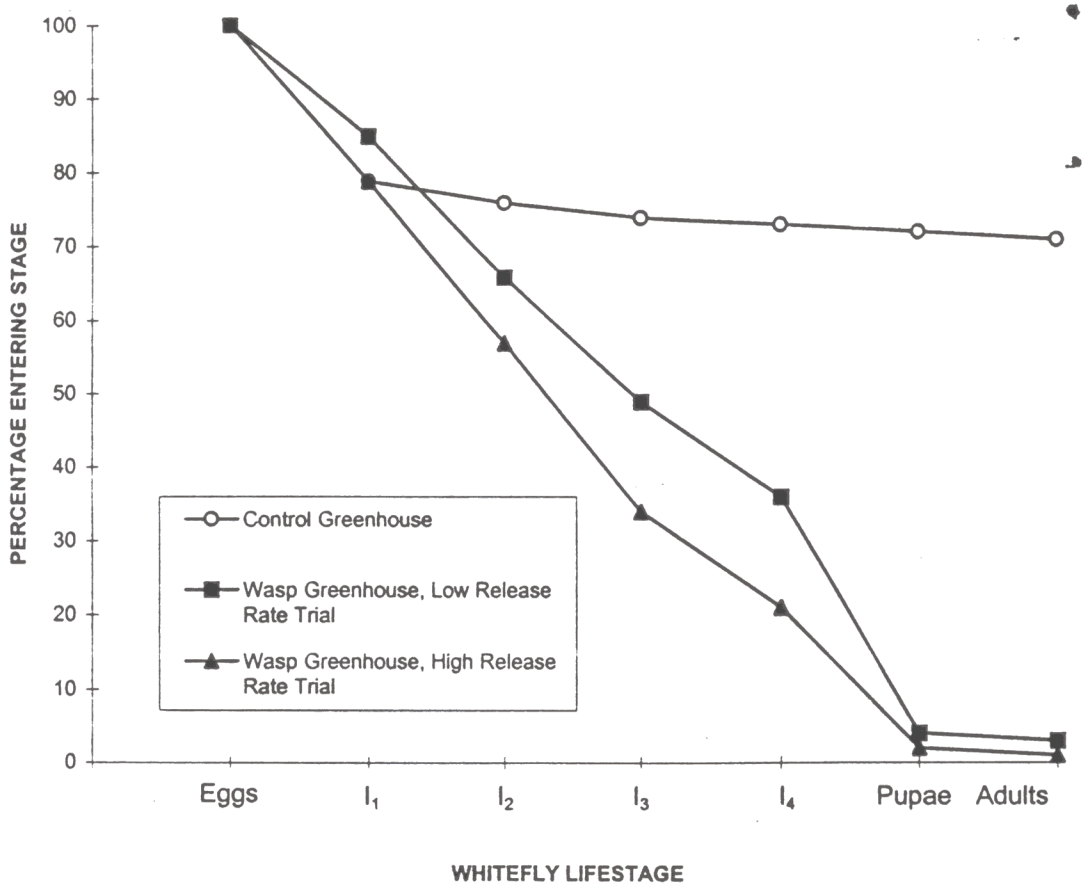

Fig. 1. Survivorship of *B. argentifolii* cohorts on poinsettia in the presence and absence of *E. formosa* Beltsville strain. Survival rate for each stage was calculated as the number entering each lifestage divided by the number of eggs at the start of each cohort (see Table 4). I_1, settled 1st instar, I_2, 2nd instar, I_3, 3rd instar, I_4, 4th instar.

from summary life-table data in Table 4 for each experimental treatment are presented in Fig. 1. Whitefly survivorship in the control greenhouse was consistently higher for each developmental stage after the 1st instar when compared with the averaged survivorship across the replicated low and high release rate greenhouses. Survivorship curves for control greenhouses show highest real mortality (d_i/l_c = death in the *i*th stage and l_c is the size of the cohort at the commencement of the generation) (Southwood 1978) occurring from egg to settled 1st instar (21%); thereafter, real mortality in successive lifestages was ≈ 1–3% (Table 4; Fig. 1).

In the presence of *E. formosa* Beltsville strain, the number of nymphs surviving to enter successive developmental stages declined rapidly after the settled 1st instar when compared with the control greenhouse (Fig. 1). In the low release rate greenhouses, real mortality was greatest from 4th-instar nymphs to pupae, where 4th-instar mortality contributed 32% to the observed total mortality (Table 4; Fig. 1). In the high release rate greenhouses, real mortality was greatest from 2nd instar to 3rd instar, where 2nd instar mortality accounted for 24% of the observed total mortality (Table 4; Fig. 1). The largest observed real mortality difference between the low and high release rate greenhouses occurred in the 4th instar, where the percentage of individuals becoming pupae differed by 13% (i.e., 4th instar mortality in the low release rate greenhouses was 32% of total observed mortality versus 19% for the high release rate greenhouses) (Fig. 1).

Net Reproductive Rates (R_o). Sex ratio, net fecundity (L_xM_x), and net reproductive rate (R_o) estimates for each whitefly cohort photographed in each treatment are presented in Table 6. Temperatures decreased over the course of the 14-wk trial (Table 6). Decreasing temperatures result in sex ratios with a lower proportion of females with lower net fecundity (Enkegaard 1993a). As a consequence of this decrease in temperature, R_o estimates for successive whitefly cohorts in the control greenhouse decreased, and they averaged 17.10 over the cropping cycle (Table 6).

In low release rate greenhouses R_o values for each successive whitefly cohort decreased, and *B. argentifolii* had an average R_o of 0.95, reflecting a 99.94% decrease from the growth rate of the control population (Table 6). The average R_o for *B. argentifolii* in the high release rate greenhouses was 0.32, a 99.98% decrease from the growth rate of the control population (Table 6).

Table 6. Mean temperature ± SE, sex ratio, net fecundity (L_xM_x), and net reproduction (R_0) estimates for *B. argentifolii* in each experimental greenhouse

Greenhouse	Cohort	Temp, °C	Sex Ratio	No. Eggs	No. Adults	No. Females	L_xM_x	R_0
Control greenhouse	1 + 2	22.36 ± 0.37	0.65	213	150	97.41	39.80	18.20
	3	21.93 ± 0.33	0.64	531	388	249.03	37.12	17.41
	4	21.59 ± 0.23	0.64	851	601	381.98	34.91	15.67
Control average	1–4	21.96 ± 0.18	0.64	1,595	1,139	731.59	37.29	17.10
Low release rate greenhouses	1 + 2	22.62 ± 0.27	0.65	308	48	31.40	41.49	4.23
	3	21.98 ± 0.18	0.64	522	15	9.64	37.43	0.69
	4	21.70 ± 0.16	0.64	831	1	0.64	35.64	0.03
Low release avg	1–4	22.11 ± 0.13	0.65	1,661	64	41.28	38.24	0.95
High release rate greenhouses	1 + 2	22.62 ± 0.28	0.65	365	20	13.08	41.49	1.49
	3	22.03 ± 0.19	0.64	470	0	0.00	37.72	0.00
	4	21.69 ± 0.16	0.64	691	0	0.00	35.59	0.00
High release avg	1–4	22.12 ± 0.13	0.65	1,526	20	12.90	38.30	0.32

Cohort, whitefly cohort from life-table; temp, average of the daily maximum and minimum temperatures ± SE experienced by each cohort across replicated treatments; sex ratio, proportion of females produced at mean temperature experienced by each cohort (estimated from Enkegaard 1993); no. eggs, total number of eggs in the cohort that was photographed (from life-tables); no. adults, total number of adults that were produced from the photographed eggs (from life-tables); no. females, estimated number of females using sex ratio estimate; L_xM_x, net fecundity per female at mean temperature experienced by each whitefly cohort (estimated from Enkegaard 1992); net reproductive rate (R_0), the total number of progeny produced by emerged females (column 6 × column 7)/number of eggs that started that cohort (column 4).

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* Beltsville strain are presented in Fig. 2. In the absence of parasitoids, densities of live nymphs and pupae increased rapidly in number after week 9 to reach an estimated final density of ≈6,000 live nymphs and pupae per plant at week 14 (Fig. 2A).

The high release rate of *E. formosa* Beltsville strain (3 wasps per plant per week) suppressed *B. argentifolii* population growth earlier than the low release rate (1 wasp per plant per week) (Fig. 2B). In the high release rate greenhouses, whitefly numbers peaked at week 6 and then declined to low levels by week 10 (Fig. 2B). In the low release rate greenhouses, live nymphs and pupae per plant peaked 5 wk later (week 11 of trial) than the high release rate greenhouses before declining to low levels by week 14 (Fig. 2B). At week 14, the average numbers of live immature whiteflies nymphs and pupae per plant in the low release rate greenhouses was 2.1 times higher than that in the high release rate greenhouses, and 0.6% that of the control greenhouse. At the same time, in the high release rate greenhouses, the average number of live nymphs and pupae per plant was 0.27% that of the control greenhouse.

Trends in Percentage Parasitism and Numbers of Emerging Parasitoids. Percentage of 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, 2 peaks in parasitism are observed at weeks 8–10 and week 14 (Fig. 3A). Peak wasp emergence in the low release rate greenhouses occurred at weeks 10 and 12, which was ≈2 weeks after peaks in parasitism. Wasp emergence at weeks 9–12 and 14 was 7–30 times higher than the number of wasps released weekly into the low release rate greenhouses. In-house reproduction by *E. formosa* Beltsville strain during the trial strongly contributed to whitefly population growth suppression after week 11 when a rapid decline in numbers of live whitefly nymphs and pupae was observed (Fig. 2A).

In high release rate greenhouses, parasitism peaked at week 9 at 57% (compared with 72% in the low release rate greenhouses at week 14) (Fig. 3B). Peak wasp emergence also occurred at week 9. Wasp emergence from in-house reproduction exceeded the weekly release rate in weeks 8–12 and 14 by 2–19 times (Fig. 3B). As with the low release rate greenhouses, wasp emergence into the high release rate greenhouses at this time strongly contributed to the decline in live whitefly nymphs and pupae after week 6 (Fig. 2B). Peak wasp emergence in the high release rate greenhouses at week 9 was 1.4 times greater than peak emergence in the low release rate greenhouses at week 12. Total wasp emergence into the high release rate greenhouses summed across all weeks was 1.2 times higher than the low release rate greenhouses.

Trends in Host to 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. The number of hosts available for attack by individual wasps steadily increased after week 1 in the low release rate greenhouses to peak at weeks 7 and 13 (Fig. 4A). In the high release rate greenhouses, the number of hosts available for attack showed at a single peak at week 6 and declined thereafter (Fig. 4A). At week 14, the average number of hosts available for attack per wasp per plant was 2.6 times higher in the low release rate greenhouses.

Average weekly trends in mortality from causes other than successful parasitism (i.e., host feeding

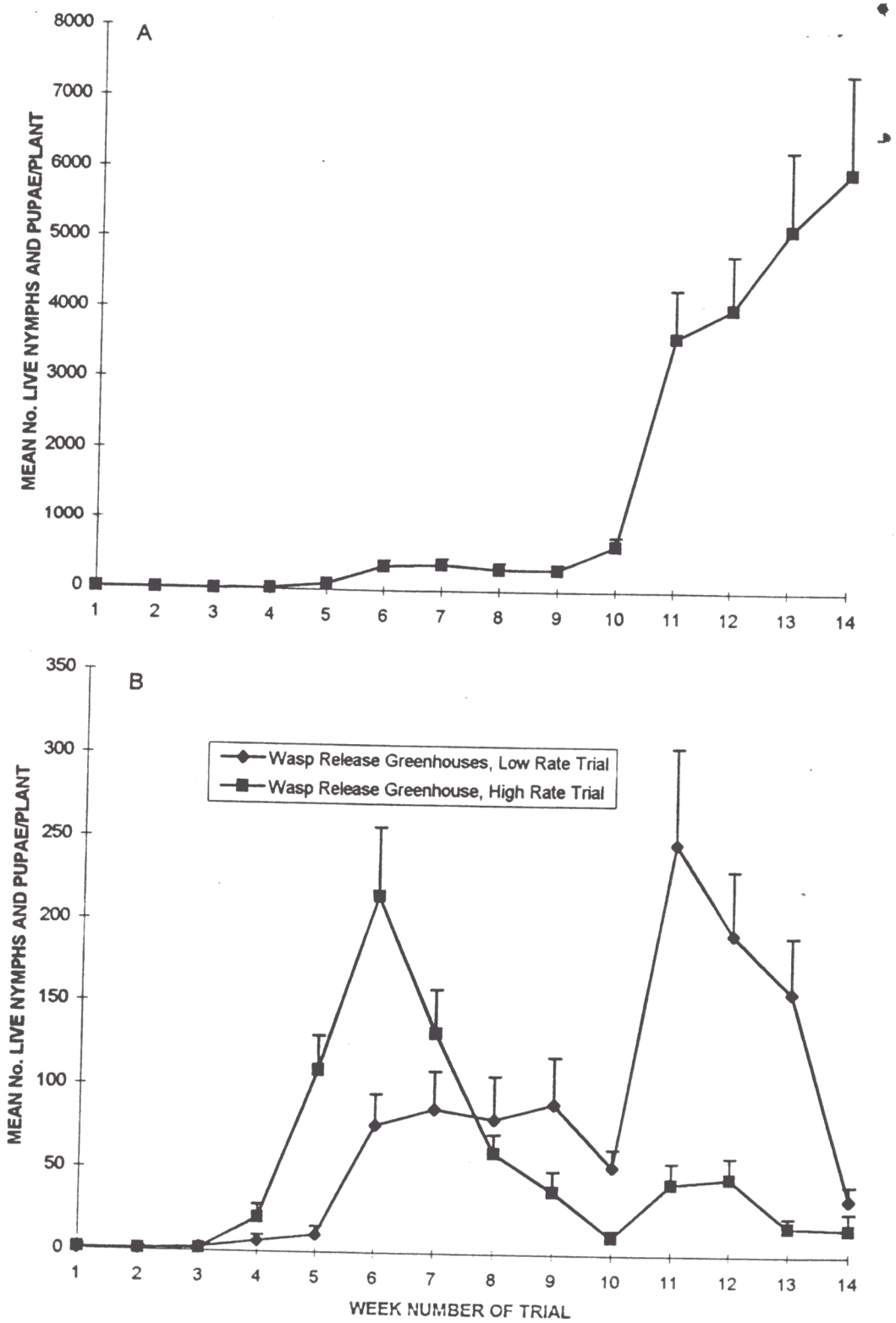

Fig. 2. Mean number of live nymphs and pupae ± SEM per poinsettia plant in the control (A) and wasp release (B) greenhouses at a low release rate (1 wasp per plant per week), and a high release rate (3 wasps per plant per week).

and aborted parasitism) for *B. argentifolii* in the low and high release rate greenhouses are shown in Fig. 4B. After week 3, percentage of mortality increased weekly to reach 91 and 96% at week 14 in the low and high release rate greenhouses respectively (Fig. 4B).

End of Crop Sales Inspection. At sale (week 14), the mean numbers ± SE of live nymphs and

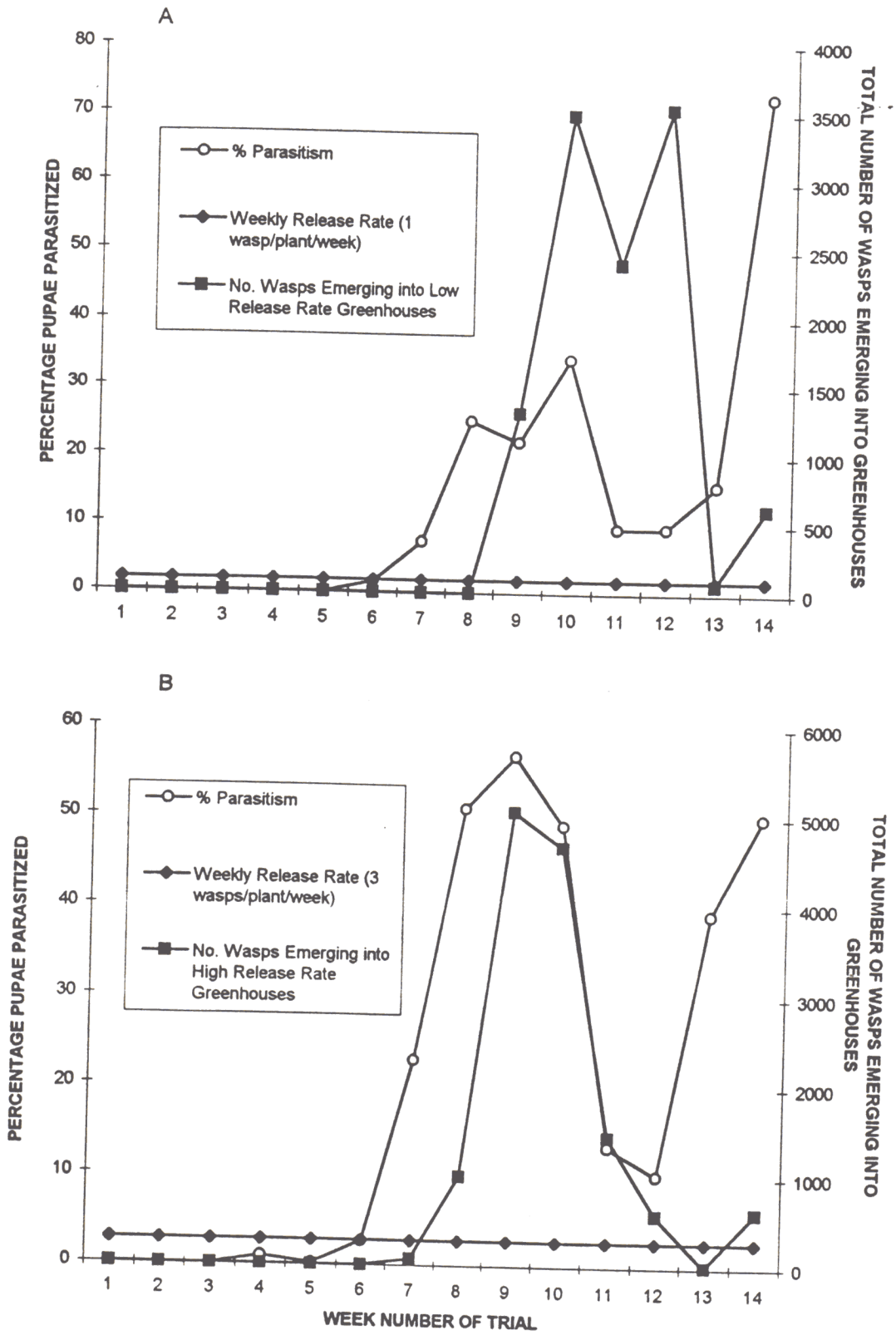

Fig. 3. Average weekly estimates of the percentage of *B. argentifolii* nymphs parasitized by *E. formosa* Beltsville strain in the low (A) and high (B) release rate greenhouses and the total number of *E. formosa* Beltsville strain emerging weekly into the low (A) and high (B) release rate greenhouses.

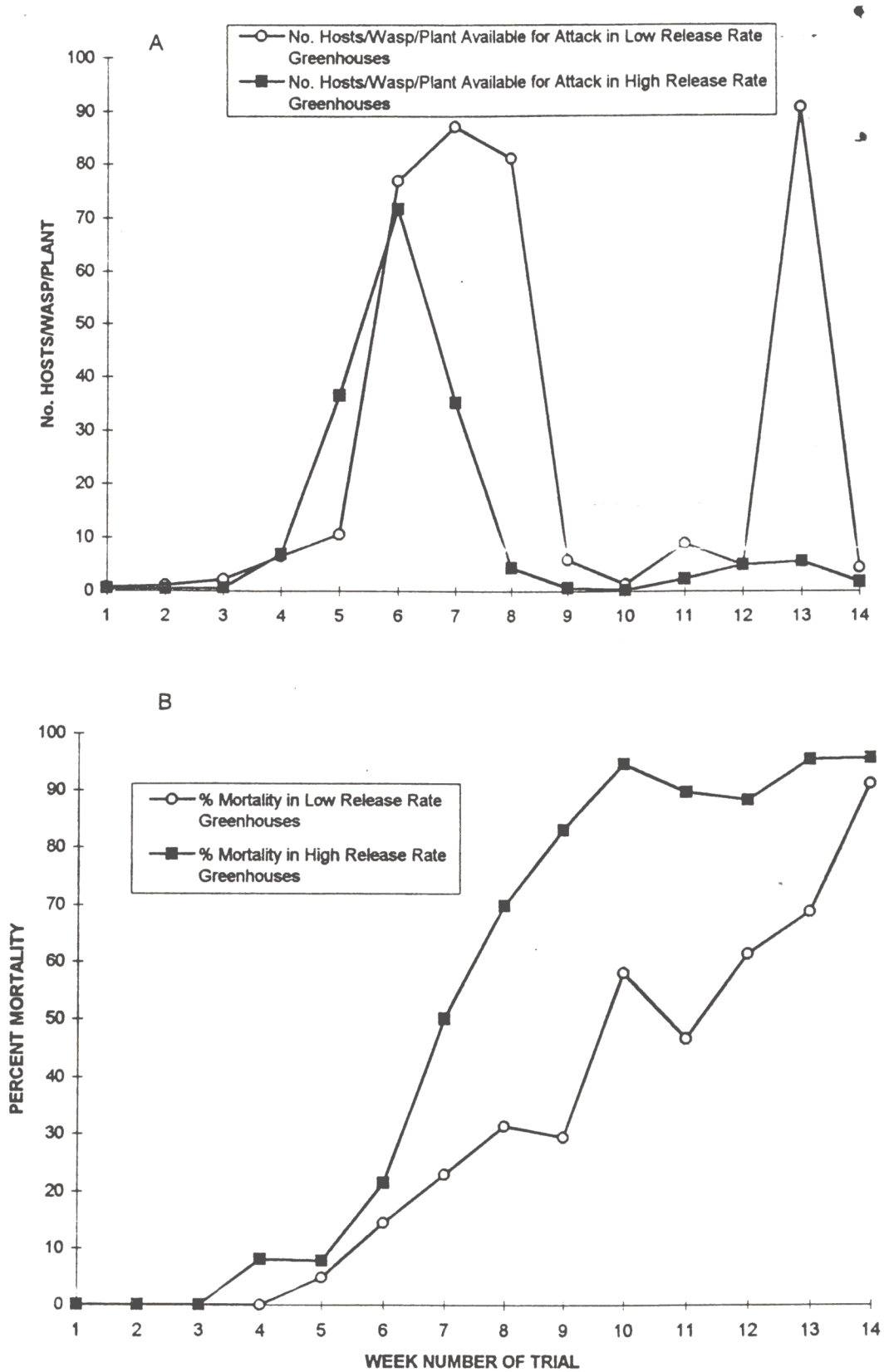

Fig. 4. The average number of susceptible *B. argentifolii* nymphs and pupae per plant (A) available for host feeding and parasitism by individual wasps (*E. formosa* Beltsville strain) for the low and high release rate greenhouses, and (B) the percentage mortality of *B. argentifolii* nymphs and pupae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

Table 7. Infestation statistics (mean ± SE) for live *B. argentifolii* nymphs and pupae on poinsettia leaves from experimental greenhouses in which *E. formosa* Beltsville strain had been released and on leaves of poinsettias collected from retail outlets at the end of the growing season

Treatment	No. plants inspected	% Plants infested	No. leaves examined	% Leaves infested	Nymphs/Leaf
Low release rate greenhouses	30	100	180	74	4.89 ± 0.56
High release rate greenhouses	30	77	180	31	0.88 ± 0.16
Five retail outlets in Amherst, MA	72	28	432	12	1.45 ± 0.36

pupae per leaf combined across replicated greenhouses were 4.89 ± 0.56 and 0.88 ± 0.16, respectively, for the low and high release rate greenhouses. The mean number of live nymphs and pupae per leaf on plants inspected in retail outlets was 1.45 ± 0.36 (infestation data from retail outlets was collected before imidacloprid was registered for greenhouse use in Massachusetts). The mean number of nymphs per leaf differed significantly between treatments ($F = 20.85$, df = 791, $p < 0.0005$). Significantly more nymphs per leaf were found in low release rate greenhouses when compared with high release rate greenhouses and insecticide treated plants. There was no significant difference between the mean number of nymphs per leaf between the high release rate greenhouses and chemically protected plants. Immature whiteflies in the high release rate greenhouses were found on a larger percentage of plants (77%) than insecticide treated plants (28%) (Table 7). This indicates that the high release rate of *E. formosa* Beltsville strain produced a poinsettia crop with similar final numbers of live immature whiteflies, but survivors were spread over a larger number of plants.

Discussion

In small experimental greenhouses at Cornell University, life-table analyses showed that *E. formosa* Beltsville strain released at 1 wasp per plant per week (low release rate) and 3 wasps per plant per week (high release rate) exerted a suppressive effect on *B. argentifolii* population growth on poinsettia when compared with greenhouses that did not receive the parasitoid (Table 4. Fig. 2). There was substantial reduction in net reproductive rates of *B. argentifolii* in greenhouses (99.94% reduction in low release rate greenhouses and 99.98% in high release rate greenhouses) into which *E. formosa* Beltsville strain was released when compared with the control greenhouse that did not receive the parasitoid (Table 6).

The high release rate of *E. formosa* Beltsville strain provided better control of *B. argentifolii* than the low release rate. At week 14, estimates of live whitefly nymphs and pupae per plant were lower in the high release rate greenhouses (Fig. 2B), and estimates of the mean number of live nymphs and pupae per leaf from the end of crop sales inspection were significantly lower in the high release rate greenhouses (Table 7). Both release rates resulted in average R_o values <1 (Table 6), which was expressed by decreasing densities of live nymphs and pupae in population counts in both the low and high release rate greenhouses. The observed population declines were faster in the high release rate greenhouses (Fig. 2B), and this trend was represented by an average R_o for the high release rate greenhouses, which was 66% lower than the low release rate greenhouses (Table 6).

Emergence by *E. formosa* Beltsville strain exceeded weekly releases by 7–39 times at weeks 9–12 and 14 in the low release rate greenhouses (Fig. 3A), and by 2–19 times at weeks 8–12 and 14 in the high release rate greenhouses (Fig. 3B). In-house reproduction of this magnitude could have resulted in the termination of parasitoid releases after week 8 in both the low and high release rate greenhouses because in-house parasitoid emergence was exceeding weekly releases. This would have reduced the number of weekly releases by 43%, and the use of in-house reproduction could reduce the cost of control.

In our experimental greenhouses we deliberately introduced whiteflies to determine parasitoid impact on *B. argentifolii* population growth. Consequently, whitefly densities were probably higher in our experimental greenhouses than those typically observed in well managed, commercial poinsettia greenhouses. High levels of parasitoid recycling within greenhouses requires there to be high numbers of whiteflies to parasitize in the crop, and in-house reproduction by *E. formosa* Beltsville strain will not be as great when fewer nymphs are available for both host feeding and reproduction. Also, increasing *B. argentifolii* densities that would be necessary for high levels of parasitoid reproduction would be unacceptable to many poinsettia growers because of the uncertainty of whether parasitoid action could reduce and maintain whiteflies at acceptable levels before bract coloration. Once bracts color, the range of chemical options for whitefly control are substantially reduced because of the risk of phytotoxicity damage to bracts. This could limit the use of *E. formosa* Beltsville strain as a biological control agent of *B. argentifolii* on poinsettia that is grown for sale at Christmas.

An alternative option would be to use *E. formosa* Beltsville strain for *B. argentifolii* control on poinsettia stock plants that are grown in the summer and from which cuttings are taken to be rooted for the fall poinsettia crop (colored plants). In this production system, growers would be able to apply

remedial insecticidal sprays if biological control failed without risk of damaging plants. Furthermore, whitefly hygiene may be less stringent if cuttings are not exported and are retained for use by the producer. This may make biological control a more attractive control option to some growers. In the trial presented here we assessed *E. formosa* Beltsville strain for *B. argentifolii* control on poinsettias grown in the fall. We have recently evaluated the performance of this wasp in summer greenhouse conditions in Massachusetts for *B. argentifolii* control on poinsettia stock plants, and these data are being analyzed.

The results of our work presented here on *E. formosa* Beltsville strain corroborate the laboratory findings of Heinz and Parrella (1994). This parasitoid appears to be a promising biological control agent of *B. argentifolii* on fall grown poinsettia.

Acknowledgments

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