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BIOLOGY AND USE OF THE WHITEFLY PARASITOID *ENCARSIA FORMOSA*

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ABSTRACT

Encarsia formosa is a parasitoid used worldwide for the biological control of whiteflies on vegetables and ornamental plants grown in greenhouses. Because of outstanding success in controlling *Trialeurodes vaporariorum* on tomatoes, the biology and behavior of this wasp have been intensively studied to identify attributes that contribute to successful biological control and how best to manipulate augmentative releases into greenhouses to suppress whitefly population growth. In this article, we review the biology of adult and immature *E. formosa*, population dynamics of whitefly-parasitoid interactions, and commercial use in greenhouses. Deficits in knowledge of aspects of *E. formosa*'s biology and use are noted.

INTRODUCTION

Encarsia formosa (Hymenoptera: Aphelinidae) is used worldwide for commercial control of whiteflies in greenhouse crops (142, 144). Commercial use

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began in Europe in the 1920s, but by 1945, interest waned owing to development of pesticides. After 1970, use of the parasitoid was reinitiated and has expanded from 100 hectares of greenhouse crops to 4800 hectares in 1993 (130, 144). Comparison of the greenhouse area in various parts of the world with the area employing biological control agents shows that most usage of *E. formosa* occurs in Europe and Russia and that the largest concentrations of greenhouse production in which *E. formosa* is not extensively used are in North America and Asia, particularly Japan (130). These are areas where increased use of *E. formosa* would be possible.

Principal greenhouse crops in which *E. formosa* is used include tomato (*Lycopersicon esculentum*) and cucumber (*Cucumis sativus*) (144). The parasitoid is also used, or being tested, to a lesser extent on eggplant (*Solanum melongena* var. *esculenta*) and gerbera (*Gerbera jamesonii*) (130), poinsettia (*Euphorbia pulcherrima*) (1, 56, 76, 90), marigolds (*Tagetes erecta*) (49), and strawberry (*Fragaria* X *ananassa*) (30).

E. formosa was described from specimens reared from an unidentified aleyrodid on geranium (*Pelargonium* sp.) in 1924 in a greenhouse in Idaho (United States) (35). There are no synonyms in the literature. Morphological descriptions of all life stages are provided by Speyer (111). Because of releases into greenhouses worldwide, *E. formosa* has a cosmopolitan distribution and its native range is uncertain. However, affinity to the *Encarsia luteola* group suggests a Western Hemisphere origin (92).

The genus *Encarsia* is in need of revision, and keys at the world level are currently lacking. A pictorial key to the 27 North American species has been prepared (104). A world key for species of *Encarsia* associated with one important pest host, *Bemisia tabaci*, is available (92).

E. formosa parasitizes at least 15 hosts in eight aleyrodid genera (92, 104). *E. formosa* is hyperparasitized by *Signiphora coquilletti*, *Encarsia pergandiella*, and *Encarsia tricolor* (5, 13, 164). Although *E. formosa* occasionally has been reported attacking whiteflies on outdoor crops (38, 80) or wild plants (39), information is not available about its ecology or population dynamics in nature.

BIOLOGY OF *E. FORMOSA*

Foraging Behavior

HOST LOCATION To reproduce successfully in greenhouses, *E. formosa* must locate potential hosts, assess host quality, and use nymphs appropriately for host-feeding or parasitism. Following release into the host's habitat (i.e. greenhouses), *E. formosa* apparently employs random searches to find hosts at all spatial scales. Infested host plants, infested leaves, and whitefly patches are found via random flight, landing, and walking sequences (136, 142, 146, 150) without visual or olfactory cues (83, 136). When searching new leaves, the parasitoid does not distinguish between upper and lower surfaces and shows no preference for centers or edges of leaves (146, 151). The rate at which hosts are encountered is dependent on the parasitoid's walking speed, whitefly size, and number of hosts on a leaf (136). Walking speed is reduced by leaf venation (136), high trichome densities (132, 136, 163), excessive honeydew (150, 156), encounters with nymphs suitable for host-feeding and parasitism (136), decreasing temperature (150), low barometric pressure (151), and smaller egg loads (120, 150).

Once *E. formosa* encounters hosts or their products in a patch, residency time on infested leaves increases 2- to 10-fold (142, 146, 150, 151). Factors that trigger increased residency times include contact with honeydew (150, 156), whitefly exuviae, parasitized hosts, and oviposition in unparasitized hosts.

Following oviposition in a patch, *E. formosa*'s tendency to change position from lower leaf surfaces (where whitefly nymphs are most common) to upper leaf surfaces is significantly reduced. Contact with honeydew does not affect the tendency of wasps to change leaf sides (146). Walking pattern and speed on infested leaves are not affected by host encounters and are the same as on uninfested leaves (142, 146, 150). Average residency time on tomato leaflets when hosts are not encountered or since last host contact is approximately 20 min. On larger leaves such as gerbera, leaf residency times average 1 h. However, there is no general correlation between increasing leaf size and residency time (151).

Patch abandonment is induced by passage of time since last host encounter (146, 150) and contact with parasitized hosts (137). When high numbers of parasitized hosts are encountered, time spent cleaning and duration of uninterrupted walking bouts increase, causing total leaf residency time to increase. Time spent inspecting hosts decreases before wasps leave (137). Potential trade-offs between leaving a patch of declining value in search of better patches and mortality risks associated with inter-patch travel have not been studied.

HOST USE *E. formosa* is a thelytokous, autogenous, synovigenic, solitary endoparasitoid that matures 8–10 eggs per day (67, 159). Daily egg maturation and oviposition rates decline as wasps age (2). Adults obtain energy and nutrients by consuming honeydew and hemolymph of hosts that are pierced with the ovipositor, but in which no egg is deposited. Killing hosts for adult nutritional purposes is termed host-feeding.

Egg load, the number of mature eggs available to a parasitoid for oviposition, and size of available hosts has been shown for some species to influence the frequency with which hosts are used for either nutrition or reproduction

(68, 78). The influence of egg load on host-feeding by *E. formosa* has not been determined.

E. formosa will host-feed on all pre-imaginal stages of *T. vaporariorum* except the egg (123), but it prefers second-instar nymphs and pupae (82, 123). However, the pupae and all nymphal instars of *B. tabaci* are used equally for host-feeding (27). To host-feed, *E. formosa* wounds nymphs or pupae by probing with the ovipositor for up to 6 min and feeds from wounds that wasps may enlarge with their mandibles (123, 135). This probing followed by feeding kills hosts (82). Nymphs that have been used for feeding are not used for oviposition, and previously parasitized whiteflies are not used for host-feeding (82).

E. formosa will oviposit in all immature stages of *T. vaporariorum*, except the egg and the mobile first instar, and in all immature stages of *B. tabaci* older than the settled first-instar nymph (12, 27, 81). *E. formosa* prefers to oviposit in third- and fourth-instar and prepupal nymphs of both *T. vaporariorum* and *B. tabaci* (12, 27, 81, 82). The rate of successful emergence of the parasitoid is highest from these preferred stages (81, 82). *E. formosa* does not oviposit in up to 50% of suitable hosts in preferred stages, even when these are not parasitized or mutilated from host-feeding. Such hosts may be parasitized at a later encounter. Failure to oviposit in such hosts may result from defensive host movements (137).

Experimental evidence is lacking as to what cues are used by *E. formosa* to determine host size. Wasps may use their antennae to obtain olfactory and resonance information about hosts, and this information, coupled with stimuli received while making 180° turns on the dorsum of the nymph, may be used to determine host size (82, 135). Behaviors associated with host searching, host selection, oviposition, and host-feeding have been described (83, 123, 135, 150).

A host of suitable size for parasitism requires further evaluation by parasitoids to determine if it has been previously parasitized. *E. formosa* avoids self-superparasitism with 100% efficiency (150), but the mechanism is undetermined. Wasps avoid superparasitism of non-self conspecifics with 90–100% efficiency, provided that immature parasitoids in hosts are larvae or pupae (137). If immature parasitoids are eggs, efficiency of discrimination is 86% (150). The mechanism for detection of non-self conspecific parasitism has not been studied, but it may involve both antennal inspection of the host and ovipositor insertion. If conspecific eggs are detected in the host, they may be pushed to one side or pierced with the ovipositor before oviposition by the second wasp (3). Experienced parasitoids superparasitize as frequently as naive females (150). In artificial arenas, superparasitism increases as the wasp-host ratio increases (15). The ability of *E. formosa* to avoid oviposition in hosts parasitized by other species has not been determined, and how wasp larvae might compete with each other within a single host is unknown following either super- or mulitple-parasitism.

Biology of the Adult Parasitoid

FECUNDITY AND LONGEVITY *E. formosa* has 5–16 ovarioles, each with up to three mature eggs (67, 143, 157–159). Ovariole number and body size (measured as head width) are positively correlated (157, 158). Numbers of mature eggs increase when the wasp has access to carbohydrates, and eggs are resorbed after three days at 20°C in the absence of suitable hosts (143). Oogenesis occurs between 10° and 40°C and is greatest at 25°C (159). All available mature eggs can be laid within 1 h, and oviposition occurs predominantly in the morning (67). Daily oviposition rates decline as wasps age (2). The morphology of the reproductive system has been described (126).

Longevity of *E. formosa* is not correlated with body size (as measured by headwidth) (143) and decreases with increasing temperature (124). At 20°C, longevity is greatest when wasps can oviposit and feed at 52 days (143). Natal plants of the host affect parasitoid longevity. In the laboratory, when honey was provided as a carbohydrate source, wasps that emerged from hosts on cucumber lived significantly longer than those from hosts on tomato or tobacco (*Nicotiana tabacum*) (143).

Both fecundity and longevity can be affected by the host from which the wasp is reared. *E. formosa* reared from a large whitefly such as *Aleyrodes proletella* have significantly more ovarioles than wasps reared from smaller hosts such as *T. vaporariorum* (158). Wasps reared from *B. tabaci* have lower fecundity and longevity compared to wasps reared from the larger host *T. vaporariorum* (122). Parasitoids foraging on poinsettia live for 9 or 12 days at 21°C when reared from *B. tabaci* and *T. vaporariorum*, respectively (122). These differences can be reduced after *E. formosa* has been reared on *B. tabaci* for 5–18 generations (9). Life-time fecundity, daily oviposition rates, and longevity at various temperatures have been determined (2, 19, 122, 124, 141, 159).

THELYTOKY Thelytoky in *E. formosa* is mediated by *Wolbachia* bacterial infections (119, 172). Exposure of females to antibiotics or high temperatures (31°C) for two or more generations (172) suppresses microbial activity, allowing females to successfully produce male offspring. Fecundity is reduced once symbionts are eliminated (119). Males develop as primary endoparasitoids of whiteflies (172). The mating behavior of *E. formosa* has been described (66); however, males are unable to inseminate females successfully (172).

ADULT DISPERSAL Flight of adult wasps in greenhouses commences 1–3 h after sunrise and is greatest in the early afternoon under both short and long day conditions (26). Flight activity is positively correlated with temperature (26) and can occur at temperatures as low as 13°C (124). At 18°C on tomato, wasps migrate up to 5 m in 90 min (124). Nocturnal flight is rare (26), and wasps will disperse shorter distances at low light intensities (less than 500 lux) than at high light intensities (greater than 8000 lux) (140). Short days and low light intensity may affect the efficacy of *E. formosa* (88).

Biology of the Immature Parasitoid

The lower thermal threshold for development of pre-imaginal stages is 10.5°–13.3°C (27, 87, 141, 149). Egg to adult eclosion requires 188.9–207 day-degrees above the thermal threshold (27, 87), and development may be faster under fluctuating temperatures (115). The upper lethal temperature for immature *E. formosa* has been estimated as 38.3°C (149).

Whitefly life stage influences *E. formosa* mortality rates and developmental times. Eggs laid by *E. formosa* successfully hatch and develop in all nymphal stages and the pharate adult of *T. vaporariorum* [pharate adult stage plus the transitional substage described by Nechols & Tauber (81) equals the "pupa" of other workers]. The parasitoid's development does not pass the first instar until the host reaches the fourth instar. *E. formosa* completes its life cycle and emerges as an adult from fourth-instar whitefly nymphs when oviposition occurs in prepupal whitefly stages, and from the pharate adult stage when oviposition occurs at the transitional substage of the pharate adult (81). Wasps that begin development in third- and fourth-instar nymphs exhibit highest survivorship, and developmental times are reduced by approximately 38% (81). Developmental rates for *E. formosa* in each nymphal stage of *T. vaporariorum* at various temperatures have been estimated (2, 149). The physiological mechanism synchronizing development of *E. formosa*'s larva with that of its host is unknown, as are mechanisms by which quiescent or developing larvae counter host defenses.

Whitefly species identity affects both mortality rates and developmental times of immature wasp stages. When *E. formosa* is reared in *B. tabaci* instead of *T. vaporariorum*, pre-imaginal mortality increases 1.3-fold to 8-fold (12, 122) and developmental time increases 22% (122).

The plant host on which the whitefly develops also affects *E. formosa* development. For seven plant species on which *Trialeurodes ricini* was reared, *E. formosa* development times were significantly longer on French bean (*Phaseolus vulgaris*) (the poorest host) than on cotton (*Gossipium hirsutum*) (the best host). Mortality of immature parasitoids did not differ between host plants in this experiment (109). At 22.5°–25°C, development of immature *E. formosa* in fourth-instar *T. vaporariorum* nymphs required 15 days on tomato (163), tobacco (2), eggplant, cucumber, and sweet pepper (*Capsicum annum*) (163). Development time is longer (24.5 days) on poinsettia (122) at similar temperatures. Survival of immature parasitoids varies significantly between poinsettia cultivars when *Bemisia argentifolii* (=*B. tabaci* strain B) is the host (50).

E. formosa pupates facing the host's venter, with its head directed towards the host's anterior (71). The prepupa excretes two to four meconial pellets along the lower margins of the host. The pharate adult parasitoid requires 25–98 min to rotate within the host to face the dorsal surface. From this position, the adult parasitoid chews a hole through the host's dorsum and emerges (71). Peak wasp emergence occurs within 4 h of sunrise (140).

POPULATION DYNAMICS

Sampling

Whitefly population densities must be estimated in order to determine when to start parasitoid releases and to measure the effectiveness of releases. Such estimations have been made with three approaches: trap counts, presence-absence ratios on inspected plants, and direct counts of whitefly stages on plants. Trap counts (as number of adult whiteflies caught per yellow sticky trap) are least precise but are widely used as monitoring tools because they are economical in terms of labor for whitefly monitoring. To detect whiteflies in the range of 0.01–0.1 adults per plant on tomato requires one trap per 180 plants (41). This system has been used with tomato crops in Canada to time initial control measures.

Presence-absence sampling plans are based on correlations of the proportion of samples bearing either healthy or parasitized whitefly stages with pest density. Such sampling has been used in cucumber (47) and tomato crops (73, 74) to monitor *T. vaporariorum* and *E. formosa* population levels.

Accuracy of direct counts of whitefly densities are influenced by their clumped distribution. Efficiency of a three-stage (plant, leaf, leaflet) system developed by Yano (169) was compared to presence-absence and trap count methods on tomato. Presence-absence sampling and trapping are the least complicated and are considered to be the most useful for monitoring *T. vaporariorum* densities (169). Rumei et al (100) analyzed several sampling plans to monitor the population densities of *T. vaporariorum* for ecological studies and found that none gave the level of accuracy (10% error, 95% confidence level) needed for such research. They attributed this deficiency to the highly contagious distribution of the whitefly.

Host/Parasitoid Dynamics

Attempts to understand the dynamic interaction of *E. formosa* with its host have been driven by the desire to predict whitefly population growth in commercial greenhouses. Secondarily, *E. formosa*'s interaction with *T. vaporariorum* has also been modeled in an attempt to identify factors that stabilize such interactions (14, 16, 17, 165, 170, 171). Factors affecting population dynamics of *E. formosa* and *T. vaporariorum* in greenhouse vegetable systems include host-parasitoid ratios, starting density and age structure of whitefly populations at time of first parasitoid releases (17, 31), levels of host-feeding and parasitism (18), temperature, and host plant (98). Methods used in these studies have included estimating correlations under non-experimental regimes between observed conditions and outcomes, conducting experiments to identify factors affecting population dynamics, and developing models to predict the dynamics of population interactions and the effects of parasitoid release regimens on whitefly population growth.

Burnett studied *E. formosa*'s interaction with *T. vaporariorum* (14, 16) and found that initial whitefly density (17) and the interaction between host-feeding and whitefly population age structure (18) strongly influenced the dynamic outcome. Van Lenteren et al (131) concluded that multiple introductions of *E. formosa* over a 16-week period were necessary to stabilize *E. formosa–T. vaporariorum* population fluctuations on greenhouse tomatoes. Foster & Kelly (31) observed that densities of *T. vaporariorum* on greenhouse tomatoes typically increased three orders of magnitude after *E. formosa* releases before declining. They concluded that an initial population density of 0.1 *T. vaporariorum* adults per leaf was the highest on tomato against which *E. formosa* releases might be commercially successful (31).

Life tables of *T. vaporariorum* in the presence and absence of *E. formosa* showed that parasitoids reduced overall whitefly survival from 68.9% to 25.1%, following inoculative release on tomato in an unheated greenhouse (65). Paired life tables for *B. argentifolii* from a commercial greenhouse in which *E. formosa* was released on poinsettia at an average rate of 6 females/plant/week showed that whitefly survival from the settled first-instar nymph to the adult was only 14% in the wasp release area, compared with 67% in caged controls that excluded *E. formosa* (56). This level of suppression did not, however, provide commercially acceptable control on this crop. Spatial effects of whitefly aggregation on whitefly population dynamics were examined by Eggenkamp-Rotteveel Mansveld et al (24, 25) by counting whitefly stages and parasitism in patches of *T. vaporariorum* on greenhouse tomatoes. In this study, *T. vaporariorum* and *E. formosa* exhibited stable dynamics because whitefly patches were not fully exterminated by parasitoids (24, 25).

Within-patch dynamics of the effect of *E. formosa* on survivorship of whitefly nymphs has also been examined. As the number of whitefly nymphs in a patch increases, the proportion attacked by individual parasitoids decreases, which exemplifies a Type II functional response. Type II responses have also been observed in the laboratory with *T. ricini* and in laboratories and greenhouses with *T. vaporariorum*, *B. tabaci*, and *B. argentifolii* (28, 34, 55, 91, 108, 168). The functional response of *E. formosa* is affected by temperature (28), sublethal insecticide residues on leaves (91), numbers of searching parasitoids in greenhouses (168), egg load, successful oviposition, and walking activity (147).

Several types of population models have been used to describe dynamics between *E. formosa* and its whitefly hosts. Yamamura & Yano (165) developed a Lotka-Volterra–type differential equation model and determined that intermediate values of the host-feeding/parasitism ratio led to the lowest *T. vaporariorum* density and the least variation in population size. A simulation model incorporating a modified disc equation to account for parasitoid functional response has been used to examine variables associated with population stability (170, 171). Stability resulted from declining parasitoid efficiency at high parasitoid densities that were due to several factors, including host-feeding and moderate levels of mutual interference between parasitoids.

A systems model to simulate the host plant–*T. vaporariorum*–*E. formosa* system was developed and used to examine the role of host plant, temperature, and parasitoid release rate on whitefly population dynamics. This model used relative age instead of physiological time to investigate the effects of varying conditions on population dynamics (98, 99). Life-history parameters for *E. formosa* and *T. vaporariorum* in relation to host plant, temperature, and, for the parasitoid, host stage were determined by van Roermund & van Lenteren (148, 149). Using this information together with observations on the foraging activity of *E. formosa*, van Roermund developed an individual-based model that simulates local searching and parasitism behavior of individual parasitoids in order to simulate parasitoid/host population dynamics in a whitefly-infested tomato crop (152).

Effect of Cropping System on Parasitoid Efficacy

PHYSICAL FACTORS Among the physical factors of potential importance to host-parasitoid dynamics are greenhouse temperature, physical spacing of a crop, and fertilization regime. Among these, most attention has been focused on effects of greenhouse temperature, mainly low temperature.

Summer temperatures in some greenhouse areas such as the northeastern United States can be at or above the maximum temperature tolerated by *E. formosa* (M Hoddle, unpublished data). *E. formosa* can survive and reproduce when daily maximum temperatures exceed 35°C for a few hours for 7–11 days (75). Survival at these temperatures is greater than that of other *Encarsia* spp. (e.g. *E. tricolor*) that have been evaluated for use in greenhouses where summer temperatures are high (4).

Low temperature regimes in greenhouses have been used to reduce production costs associated with fuel consumption. Optimal greenhouse temperature for *T. vaporariorum* control with *E. formosa* is around 23°C (51). However, van Lenteren and colleagues (133) in reviewing the literature stated that the parasitoid might perform better at lower temperatures than previously thought. Control by *E. formosa* was effective when 8 parasitoid pupae per plant were introduced every 2–3 weeks when nocturnal temperatures were 5°, 8°, or 11°C on tomato in Japan (166). Releases of *E. formosa* suppressed whitefly populations by week 13 when greenhouse temperature was maintained at 18°C in the day and reduced to 7°C at night in trials on tomato in the Netherlands (62). Values of intrinsic rates of increase for *E. formosa* at several temperatures (12°, 15°, and 24°C) have been compared to those for *T. vaporariorum* to estimate the ability of *E. formosa* to suppress the whitefly under reduced temperature regimes on tomatoes (134). Enkegaard (27) determined developmental time and juvenile mortality of *E. formosa* parasitizing *B. tabaci* on poinsettia at 16°, 22°, and 28°C. Intrinsic rates of increase for *E. formosa* were greater than those for *T. vaporariorum* and *B. tabaci* at the temperatures tested (27, 134).

Physical factors such as greenhouse size and interplant spacing of the crop may also affect parasitoid foraging efficiency. Biological control is less stable in smaller greenhouses (<1000 m^2) (24, 25, 101, 142). A suggested reason for this lower stability is that in small greenhouses, releases of parasitoids often achieve higher initial wasp-whitefly nymph ratios and at these higher ratios host-feeding and superparasitism reach high levels, which result in extinction of pest and parasitoid (24, 25, 101). Reinvasion of greenhouses by whiteflies and subsequent uncontrolled pest population growth may then result (142).

Crop fertilization can sometimes disrupt the controlling action of natural enemy populations if pest populations experience greater increases in their population growth rates owing to increased nitrogen in their diet than their natural enemies do. For *B. tabaci*, fertilization of poinsettia plants did not affect whitefly developmental time but did reduce mortality of immature stages (7). Fertilized poinsettia plants (which received either calcium nitrate or ammonium nitrate) infested with *B. argentifolii* attracted more *E. formosa* (Beltsville strain) adults than unfertilized controls, and wasps on fertilized plants in a no-choice experimental design killed more whiteflies through host-feeding than on unfertilized control plants (8). However, long-term effects of fertilization on the population balance between whiteflies and parasitoids have not been investigated.

PLANT FACTORS Among the plant factors that might affect the efficacy of *E. formosa* are plant species, variety, morphological features such as trichome number and kind, and increases in canopy size over the cropping period.

Greenhouse whitefly control with *E. formosa* is good on tomato and sweet pepper, poor on cucumber, and intermediate on eggplant (145, 163). At least two factors contribute to these outcomes: the quality of the plant for growth of immature whiteflies and the suitability of the plant surface for parasitoid foraging. Tomato, for example, is a relatively poor host for whitefly development, and its leaves are suitable for parasitoid foraging. These factors together confer a population advantage to the parasitoid (163). In contrast, cucumber is a more favorable host for *T. vaporariorum*, and its leaves are less suitable for parasitoid foraging because of retentiform venation and large trichomes (163).

Within crops, cultivars may vary in their effects on the interactions between parasitoid and whitefly populations. Among 12 tomato cultivars, few differences in parasitism rates were found; however, some evidence suggested greater suitability of one cultivar for the whitefly (45). Among 5 poinsettia cultivars, those with lower trichome densities, such as Annette Hegg Brilliant Diamond, supported higher levels of host-feeding and parasitism by *E. formosa* than did other cultivars (50). Cotton varieties with low trichome density and an alternate leaf shape (termed okra) supported higher parasitism levels by *E. formosa* and lower densities of *B. tabaci* (110).

The plant feature investigated most often in relation to parasitoid efficacy has been the density of leaf trichomes (63, 100, 121, 132). Crop cultivars with low trichome densities have been found to be more favorable than those with high densities in cotton (110) and cucumber (132). On *G. jamesonii* cultivars with trichome densities from 80–1000 per cm^2, no differences could be detected in parasitoid foraging abilities (121). Comparisons across crop species showed that parasitoid walking speed (which correlates positively with foraging success) was greatest on species with lower trichome density (63). Glandular trichomes that exude sticky or toxic materials are particularly unfavorable to parasitoid foraging (22).

When *E. formosa* is used where little in-crop reproduction is expected and parasitoid density depends on weekly releases, simple growth of the crop plant will strongly influence the effectiveness of the parasitoid. Increase in the canopy volume to be searched by parasitoids will lower the parasitoid-to-leaf area ratio progressively if weekly releases remain constant (55).

COMMERCIAL USE

Mass Rearing, Product Control, and Storage

E. formosa was first mass reared for *T. vaporariorum* control in England in 1927, and by 1930, 1.5 million parasitized whitefly nymphs were produced annually and distributed on tomato leaves (112, 113). Details of mass rearing systems for *E. formosa* are available (105, 106). Tobacco is currently the host plant commonly used for commercial production (95). Parasitized *T. vaporariorum* nymphs were originally distributed on plant material (113), but problems associated with this practice [e.g. distribution of pests or diseases on leaves (95)] led to the development of other distribution methods. Currently, parasitized whitefly nymphs are removed from leaves by brushing (106) or washing (93) and glued to cardboard strips for distribution (95).

Failure of biological control with *E. formosa* has sometimes been associated with use of parasitoids of poor quality (129) or inconsistencies between numbers of parasitoids ordered and numbers received, which affect release rates (103). Quality control tests for *E. formosa* have been designed to determine if mass-reared wasps can fulfill their intended role after release into greenhouses (128, 138). Product control standards for companies that mass produce natural enemies have been developed (129, 139), and in several European countries, registration of natural enemies for pest control is contingent on availability of quality and efficacy data (129).

Quality assessment for *E. formosa* includes validation of quantities of parasitized nymphs shipped and emergence rates, adult size, fecundity, and flight ability (95, 138, 139). Testing just before shipping is recommended (139).

Cold storage of parasitized pupae following harvest is possible and may be necessary in some instances (107). Parasitized pupae can be stored at 9°–12°C for 15–20 days without affecting adult emergence rates (36). Storage at low temperatures (9°C) for more than 5 days, however, reduces adult longevity and fecundity (37).

Methods of Use

RELEASE METHODS Four distinct methods of releasing *E. formosa* into greenhouses for whitefly control have been suggested. Three of these ("pest in first," "dribble," and "banker plants") are inoculative in nature and establish a reproducing parasitoid population, after which releases are discontinued. The fourth approach, in which repeated parasitoid releases are made throughout the cropping season, is used when a reproducing population of parasitoids is not expected to develop, either because the cropping season is too short or the whitefly or host plant are unfavorable. In these cases, whitefly mortality results from host-feeding or superparasitism (55, 58).

The pest-in-first method begins with the deliberate introduction of adult whiteflies into greenhouses at a fixed rate [e.g. two whitefly adults per tomato plant (42)]. *E. formosa* is later introduced one to three times at a standard rate [e.g. eight parasitized nymphs per tomato plant (42)] at regular intervals that coincide with availability of host stages suitable for parasitism (42, 88). This method has not been widely adopted because of concern over releasing pests onto the crop.

With the dribble method, parasitoid introductions begin at planting in anticipation of natural development of a whitefly population (42, 88, 118). Regular parasitoid releases at a low rate (e.g. one parasitized nymph per plant) continue until parasitized nymphs are found in the crop (42).

The banker plant system utilizes established breeding colonies of whiteflies and parasitoids on earlier grown plants from which wasp and whitefly disperse into the crop (114). Banker plants are introduced at a fixed rate [e.g. 1 banker plant per 352 crop plants (114)]. Mesh screens can be used to cage banker plants to contain whiteflies while allowing the smaller adults of *E. formosa* to migrate into crop production areas (10).

Inundative programs require regular releases of high numbers of *E. formosa*; establishment and reproduction of the parasitoid in the crop are not expected. This method is applied most frequently to ornamental crops (55, 56, 90).

EFFICACY OF RELEASE RATES AND METHODS The pest-in-first, dribble, and banker plant techniques have provided successful control of *T. vaporariorum* on cucumber and tomato crops (42, 88, 114, 118). Success in these cases has been defined in relation to levels of sooty mold (*Cladosporium* sp.) contamination of foliage and fruit. If at harvest sooty mold levels are within commercially acceptable limits, adequate control of *T. vaporariorum* is considered to have been achieved.

In floral crops, the presence of whiteflies at even very low densities [e.g. >0.02–0.03 nymphs per cm^2 in poinsettias (M Hoddle, unpublished data)] is considered damaging, and market standards require greater levels of whitefly suppression than are used for vegetable crops [e.g. 7.0 nymphs per cm^2 in tomato (64)]. Consequently, use of *E. formosa* has been more extensive on vegetables than on floral crops (89, 144).

Inundative releases of *E. formosa* have been successful in some instances for control of *T. vaporariorum* on poinsettia (76). Control of *B. argentifolii* with weekly releases of more than three adult parasitoids per plant per week, has not been accomplished (56, 90). However, control of this whitefly species has been reported with lower weekly release rates (under two parasitoids per plant) (97, 117), or when *T. vaporariorum* co-occurred in the crop (1). In one study, as the number of parasitoids released per plant increased, parasitoid efficacy decreased, and *B. argentifolii* survivorship increased (60).

Effective testing of parasitoid release strategies and rates requires the use of replicated treatments in independent greenhouses (e.g. 55, 58, 59, 88, 118) and the use of experimental controls either in cages (e.g. 56, 90) or separate greenhouses (e.g. 55, 58, 59). Whitefly populations in control areas that develop in the absence of *E. formosa* provide comparisons with whitefly densities in biological control or chemically treated greenhouses (e.g. 55, 56, 58, 59). These comparisons provide explicit measures of whitefly suppression [e.g. comparative life tables (e.g. 55, 56, 58, 59), whitefly densities, and crop quality (e.g. 42, 56, 88, 90, 114, 118)].

Observations from experiments in which treatments were unreplicated (e.g. 42, 56, 90, 114), lacked controls (e.g. 42, 88, 114, 118), or lacked comparisons with whitefly populations treated with insecticides under commercial growing conditions (e.g. 42, 114, 118) are not useful in determining the magnitude and variability of suppression of whitefly population growth by *E. formosa*. Efficacy and cost effectiveness of parasitoid releases can be determined by comparing whitefly densities on plants subjected to prevailing insecticide practices (56, 58–60). Furthermore, percentage parasitism estimates as indicators of the attained levels of control should be used cautiously because they can be unreliable (125).

Integration of E. formosa *into IPM Programs*

IPM MONITORING AND GROWER TRAINING Use of *E. formosa* in the production of greenhouse crops has been most successful where grower support services are available. Training growers in monitoring, correct use of biological control agents, and techniques for integrating wasp releases with other control measures have been essential activities. Such training begins with making available descriptions of the pests and their management with the biological control agents (57). More specific information on topics such as integration with pesticides (e.g. 69, 116) and monitoring techniques (41, 47, 74) is required. Simple models for making decisions about need for and timing of parasitoid releases (57, 86) can be useful. Guidance on ordering and release of parasitoids is of value to growers not previously experienced in the use of biological control (57). Adoption by growers can be encouraged by demonstrations that provide growers opportunities to observe field trials (72).

INTEGRATION WITH OTHER CONTROL METHODS Use of *E. formosa* may require integration with other controls for whiteflies or other pests. Techniques with which *E. formosa* releases might need to be combined include cultural control, use of other biological control agents, and pesticides.

Cultural practices The principal forms of cultural control that can be combined with releases of *E. formosa* are inspection of new plants, sanitation, monitoring, and use of yellow sticky traps. New plant inspection is intended to identify infested plant materials before they are introduced into the greenhouse. Incoming materials should be examined, and, if possible, infested plants isolated and treated with compatible controls before placement with other plants. Sanitation (e.g. weed control and roguing infested plants) eliminates sources of whiteflies. Monitoring is necessary to enable growers to identify developing pest infestations early and to treat localized pest populations before they are spread by plant movement or plant disposal in composting areas, from which pests might invade previously uninfested greenhouses. Yellow sticky traps, in addition to use in monitoring whitefly populations, may be used as control measures to trap out small whitefly populations (153, 155, 162). In tomato (11, 153, 155) and eggplant (11) crops, traps enhanced whitefly control while allowing percentage parasitism to increase, although some authors felt the increase in pest control from the addition of traps was slight compared to control by parasitoid releases alone (167). Screening materials can prevent pests entering greenhouses through intake vents (10).

Other natural enemies Other natural enemies of greenhouse whiteflies have been examined as agents that might either be combined with releases of *E. formosa* or might be substitutes for *E. formosa* to enhance efficacy of biological control for whiteflies. Agents considered for use in combination with *E. formosa* include several species of entomopathogenic fungi and a predacious bug and beetle. Among the fungi, most attention has been focused on *Aschersonia aleyrodis* (32, 33). Selectivity of this species has been observed in that fungal spores do not infect parasitized whiteflies bearing immature parasitoids older than three days (33) and foraging parasitoids rarely oviposit in whiteflies infected by the fungus (32). This species appears to be compatible with use of *E. formosa*. Other fungal species of interest for combination with parasitoid releases include *Verticillium lecanii* (96) and *Paecilomyces fumosoroseus* (154). In Europe, *E. formosa* has been used with the mirid, *Macrolophus caliginosus* until this predator exerted an effect on whitefly population growth (102). Another predator, the coccinellid *Delphastus pusillus*, has been tested for compatibility with use of *E. formosa* and found to be valuable in suppressing high density whitefly patches (48).

Various other species of aphelinids have been considered as alternatives to *E. formosa*. Among these have been *Eretmocerus* spp. (23, 58, 160) and two hyperparasitic species, *E. tricolor* (4, 6) and *E. pergandiella* (13, 160). Models suggest that the efficacy of biological control is reduced if heteronomous and primary parasitoids such as *E. formosa* are used together (77). No definitive study has provided data on this issue.

Integration of controls for several different pests has also been of concern. Where use of *E. formosa* for whitefly control is practiced, biological controls for other pests such as leaf miners (79, 144), fungus gnats (46), aphids, spider mites, and thrips (144) may also be needed.

Pesticides More than 70 articles have been published that examine interactions between *E. formosa* and one or more pesticides, either in laboratory tests or under conditions of practical use in greenhouses. Standardized methods for determining the effects of pesticides on *E. formosa* have been developed

(43, 61, 84). The effects of more than 100 different compounds on *E. formosa* have been determined (see especially 52, 70, 85). Selective materials of interest for possible combination with *E. formosa* include insecticidal soap (94), buprofezin (40), azadirachtin (29), abamectin (173), and resmethrin (86).

GENETIC IMPROVEMENT Genetic improvement to *E. formosa* has been attempted with regard to insecticide resistance (20, 161), increased fecundity (157, 158), and improved performance on *B. tabaci* (53, 54). Efforts to select for resistance to bioresmethrin, deltamethrin, and parathion failed (20, 21). Selection for resistance to lindane was partially successful (161). Selection for increased ovarial number was not successful (157, 158). Populations of *E. formosa* exhibit differential reproductive performances on whitefly hosts, with some wasp populations outperforming others on a particular host (9, 50, 53, 54). Variation between *E. formosa* populations in levels of parasitism and host contact times on *B. tabaci,* for example, may be due to genetic factors (54) rather than conditioned responses to hosts from which wasps eclosed (53). Development of molecular techniques to identify strains of *E. formosa* would be useful.

ECONOMICS Few data are available that measure the cost of using biological control compared with other forms of whitefly control. Assessment of use on tomato concluded that beginning *E. formosa* releases early was the most secure method of control, but it was often unjustifiable economically (88). Danish growers preferred biological control of whiteflies in cucumber and tomato and perceived biological control to be less expensive than insecticides (44). Comparison of control costs on vegetables in Europe found *E. formosa* use to be less expensive then chemical control (127). On poinsettia in Germany, releases of *E. formosa* were found to be about two thirds the cost of chemical control (1). In Massachusetts, however, releases of *E. formosa* combined with insecticide applications were 9.5 times more expensive than the use of insecticides alone to produce a marketable crop (56).

CONCLUSIONS

E. formosa is widely employed for control of whiteflies on greenhouse crops, especially vegetables, and factors contributing to successful biological control have been identified. First, whitefly population growth is reduced when *E. formosa*'s intrinsic rate of increase is greater than the host's intrinsic rate of increase in the presence of parasitoids. This situation arises when host plants facilitate parasitoid searching and exhibit partial resistance to whitefly development. Second, giving-up time on infested leaves increases when hosts or host products are located, increasing the likelihood that parasitoids will encounter suitable hosts in a patch. Third, spatial refuges for whiteflies from parasitoids exist in large greenhouses (>1000 m^2), thus promoting stable host/parasitoid dynamics.

Although many aspects of *E. formosa*'s biology have been well studied, significant gaps in our understanding of this parasitoid still exist. For example, little is known about *E. formosa*'s ecology in nature, the influence of egg load on host-feeding, what cues are used to determine host stage, and how larvae affect the cellular immune responses of a wide range of whitefly hosts.

At present, biological control of whiteflies on ornamentals with *E. formosa* is generally not commercially feasible. Further research is needed to improve our ability to use *E. formosa* inundatively to produce ornamental crops with very low whitefly densities at harvest. One avenue of investigation would be to adjust release rates and timings to compensate for differences in foliage and pest density and for changes in levels of parasitism over the growing season. Several strains of *E. formosa* obtained from various localities around the world are currently in culture. Development of molecular techniques for strain identification and efficacy trials against *B. argentifolii* on greenhouse ornamentals with these parasitoids are needed.

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