

## Trichogrammatid Egg Parasitoids as a Component in the Management of Vegetable-Crop Insect Pests

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*The integration of Trichogramma spp. into pest management programs for large-scale commercial vegetable production has not been a simple process. Initially, key problems with environmental factors such as temperature and humidity were significant impediments to success. Historical difficulties with species or strain selection, the temporary host deprivation common in many agricultural fields, and interference among competing parasitoids also can be problematical. Substantial reductions in parasitoid quality (longevity, searching ability, etc.) have been documented in cases where eggs are superparasitized. In addition, pest management programs have suffered from complications resulting from incompatibility of Trichogramma spp. and pesticides. Development of crops with host plant resistance to pest insects has not always been compatible with releases of Trichogramma spp. Nonetheless, there are strategies for selecting appropriate species and strains and integrating the parasitoids with other control approaches. Most researchers agree that the key factors for species-strain selection for an inundative release program include acceptance of the host plant for foraging, acceptance of the host insect, tolerance for local environmental conditions, ability to parasitize eggs of varying ages, and searching efficiency and behavior. These species-strain selections can be integrated with other control strategies because a significant number of pesticides have a minimal impact on Trichogramma spp. Several case studies of fresh-market tomatoes are available that provide documentation of the potential benefits and economic impacts of mass releases of Trichogramma spp. in coordination with other pest control strategies. The value of such releases of T. pretiosum in tomatoes has been recognized commercially, and the practice is now in significant practical use in the tomato industry of Mexico.*

Historically, high-value crops such as vegetables with stringent cosmetic standards have been considered poor candidates for biological control programs (Biever and Hostetter 1978). As a result, most growers have relied on frequent applications of conventional pesticides. However, some recent successes in integrated pest management (IPM) programs for vegetables have included the use of parasitoids or pathogens. Examples include parasitoids for suppression of *Liriomyza* spp. (Johnson et al. 1980, Trumble 1990) or *Helicoverpa* spp. (Alvarado-Rodriguez 1988, Elizondo-Alapisco and Alvarado-Rodriguez 1988) and pathogens for control of *Leptinotarsa decemlineata* Say on potatoes (Ghidiu and Zehnder 1993, Zehnder 1994), *Plutella xylostella* (L.) on cole crops (Groeters et al. 1993, and papers therein, Tabashnik et al. 1993), and *Spodoptera exigua* (Hübner) on tomatoes (Trumble et al. 1994). These successes have positively affected grower perceptions of alternative strategies. This type of positive example, along with increasing concerns regarding pest suppression failures associated with the development of pesticide resistance (Brewer and Trumble 1991, 1993; Georgiou and Lagunes-Tejeda 1991) and fears of potential environmental damage or human health problems related to pesticide use, have led to an increase in legislation restricting pesticide availability (Trumble 1990). This legislation has subsequently stimulated vegetable producers to reevaluate all available pest management strategies, including those such as biological control that previously were considered inefficacious or uneconomical.

This chapter focuses on the use of mass-reared *Trichogramma* spp. for control of insect pests in vegetables. Because Yu and Byers (1998) have included a discussion of the potential for incorporating *Trichogramma* spp. into pest management programs for corn, the extensive literature on this topic will not be incorporated here. Likewise, early studies on inundative releases of *Trichogramma* spp. summarized in review articles by Stinner (1977) and Smith (1996) will not be discussed. The research examined in this chapter has been selected to illustrate the intensity of effort and scope of the research achievements of the past 15 yr relating to release of *Trichogramma* spp. in vegetable crops, with special reference to tomatoes.

### Problems in Integration of Parasitoids Into Vegetable Crop IPM

**Humidity and Temperature as Environmental Factors Affecting Success.** Environmental factors such as relative humidity and temperature can affect the commercial success of *Trichogramma* spp. in vegetable pest management. For example, Gross (1988) determined that exposing immature *Trichogramma pretiosum* Riley to relative humidities above 80% or below 40% adversely affected both eclosion rates and occurrence of non-functional (brachypterous) wings. However, potential population reductions for parasitoids reared in areas with relative humidities in excess of 80%

might be mitigated by an increase in fecundity observed for females developing in these conditions (Calvin et al. 1984). When exposed to temperatures exceeding 38°C, eclosion of *T. pretiosum* was reduced by greater than 70% (Gross 1988). In addition, adults that successfully emerged had a high frequency of brachypterous wings, often exceeding 50%. Although the optimum temperature for eclosion of *T. pretiosum* on eggs of 2 vegetable crop pests ranged from 30 to 32°C, fecundity was highest below 30°C (Calvin et al. 1984, Gross 1988). In contrast, emergence of *Trichogramma chilonis* Ishii developing in *P. xylostella* eggs was optimal at 20°C but decreased dramatically at 32°C (Miura and Kobayashi 1993).

The potential success of a *Trichogramma* spp. release program also may be influenced by temperature effects on the sex ratio of progeny. Bowen and Stern (1966) documented a uniparental race of the generalist species *Trichogramma semifumatum* (Perkins) (probably *T. pretiosum*), which consists almost entirely of females when reared at temperatures below 25.6°C. However, when temperatures are raised to 32.2°C or higher, >97% of the progeny are sterile males. The sex of the offspring is determined by the temperature to which the female is exposed during the adult stage. Similarly, populations of *Trichogramma cordubensis* Vargas & Cabello that were thelytokous at 20°C became arrhenotokous at 28°C (Cabello-García and Vargas-Piqueras 1985). As in the previous study, the critical exposure to temperatures affecting sex ratio occurred during the adult stage of the mother rather than during development of the immature stages. Initially, one might assume that such temperature-induced changes in the sex ratios of offspring would have obvious negative implications for biocontrol programs. For example, if temperatures frequently, or even occasionally, reach 28°C, a switch from thelytokous to arrhenotokous reproduction might reduce parasitization efficiency of subsequent generations by reducing the proportion of females. However, a recent laboratory study has shown that these temperature-induced changes may benefit augmentative control programs; the arrhenotokous females were more fecund and produced at least as many daughters as their thelytokous counterparts (Stouthamer and Luck 1993). Thus, variations among locations in environmental conditions such as temperature or relative humidity have significant implications for predicting whether a particular species of *Trichogramma* will provide a level of control adequate for commercial production.

Finally, exposure to relatively short temperature shocks during release can have a substantial impact on effectiveness of parasitoids. As reported by Chihrane et al. (1993), some *Trichogramma brassicae* Bezdenko are packaged for release in capsules. This mechanism (as well as some other release techniques) can expose the insects to relatively high temperatures, particularly if releases are made during the daylight hours. Their studies indicated that such temperature shocks reduced emergence rates as well as subsequent adult longevity and fecundity. They calculated that releasing

pupae subjected to 6-h exposures of  $\geq 35^\circ\text{C}$  resulted in at least a 50% reduction in efficiency of parasitization. In addition, the potential for establishment of these parasitoids was greatly reduced by an alteration of the sex ratio of progeny resulting from the treated wasps, which was strongly skewed to males (>85%).

#### Selection of Effective Species–Strains for Use in Vegetable Crops.

Because of the species- and strain-specific interactions of temperature and relative humidity on emergence, sex ratio, behavior, and fecundity, determining the usefulness of a species or biotype of *Trichogramma* has been the subject of considerable study. Unfortunately, species identification can be problematical. The considerable confusion regarding systematics of the genus *Trichogramma* has recently been discussed in detail (Pinto and Stouthamer 1994) and is not repeated here. However, the reader should be aware of some of the key problems confounding identification, as follows: (1) there are large numbers of phenotypically similar species; (2) many species names are incorrect or have been applied inconsistently; (3) male genitalia, historically the key morphological characteristic used to separate species, cannot be used on thelytokous forms; and (4) the mode of reproduction (arrhenotoky, etc.), which also has been used to distinguish certain species, is now known to vary with rearing conditions as well as with the presence of maternally inherited microorganisms (Smith and Hubbes 1986, Stouthamer et al. 1990, Pinto and Stouthamer 1994).

Assuming that species identification has been achieved, many authors have shown that selection of the most appropriate species or strains within species can have a substantial effect on efficiency of parasitization in a given plant–pest system (van Dijken et al. 1986 and references therein). Probably the first researchers to suggest and then comprehensively test a set of criteria for selection of *Trichogramma* spp. and strains for a specific locality were van Lenteren and his colleagues (van Lenteren et al. 1982, Pak and van Lenteren 1984, Pak et al. 1986, van Dijken et al. 1986). They discuss many of the criteria listed below in some detail. In addition, they suggested evaluating strains–species using as criteria percentage of females actively searching and parasitizing hosts, numbers of eggs parasitized, and preference (measured as acceptance/contact ratios) for different hosts. Hassan (1989) developed a similar evaluation scheme based on a choice test between eggs of pest species and the host eggs used to mass-rear the parasitoids. He also suggested using a preference test that evaluated number of contacts and number of eggs parasitized, as well as fecundity. All of these approaches were designed as an initial screen for possible candidates and were intended to complement rather than replace field evaluations.

Most authors agreed that the key factors for species–strain selection for an inundative release program include acceptance of the host plant for foraging, acceptance of the host insect, tolerance for local environmental conditions, ability to parasitize eggs of varying ages, and searching effi-

ciency/behavior. As noted by Pak and van Lenteren (1984), reproductive capacity and synchronization with the host may not be critical because these factors can be adjusted by release rates and timing of release. In addition, we note that although host suitability and host preference are desirable traits for sustained control, these traits are not always necessary if inundative releases are contemplated in short-term vegetable crops. Therefore, *Trichogramma* spp. may be used in an inundative release to replace chemical pesticides in a rapid pest management response to a synchronized (generational) oviposition event, thus minimizing the importance of host suitability. Clearly, host preference plays an important role where several acceptable pest species are present (van Dijken et al. 1986), but this measure of potential success may be less critical when only 1 target species is available. Certainly many pest species have shown strong preferences for one plant species over another, but when offered no choice in a large-scale commercial planting of the least preferred plant, large and economically damaging populations have developed (Eigenbrode and Trumble 1994). However, Wührer and Hassan (1993) reported that host egg preference has provided a significant indication of success in several studies on the biological control of *P. xylostella* in *Brassica* crops. Still, as correctly noted by Wührer and Hassan (1993), some of those *Trichogramma* spp. exhibiting lower degrees of host preference also may be viable candidates for inundative release programs. Thus, using preference as the sole, or perhaps even the primary, rationale for selection does not assure that the most suitable strains or species will be identified.

**Effects of Temporary Host Deprivation and Host Density.** Published studies that have provided more than circumstantial evidence regarding effects of host deprivation on life history parameters of *Trichogramma* spp. are few. In practice, extended periods of host deprivation are likely to be common if releases are made at low host densities as suggested by Hassan (1993).

Because some *Trichogramma* spp. are proovigenic (Pak and Oatman 1982), the lack of egg resorption during periods of low host availability could substantially affect their usefulness in a biological control program. For example, in a series of laboratory studies with *T. brassicae*, Fleury and Boulétreau (1993) documented that periods of host deprivation lasting  $\geq 4$  d resulted in  $>50\%$  reduction in the number of hosts parasitized. Similarly, Hohmann et al. (1988) determined that *Trichogramma platneri* Nagarkatti parasitized fewer hosts following a period of host deprivation. For *T. brassicae*, host deprivation did not negatively affect female longevity, sex ratio of the progeny, or rate of emergence from parasitized eggs (Fleury and Boulétreau 1993). This was not the case for the synovigenic species *Trichogramma minutum* Riley because there was a positive correlation between reproduction and longevity (Bai and Smith 1993). However, as the parasitoids aged, a gradual shift toward production of more males was observed.

This latter study did agree with the report of Fleury and Boulétreau (1993) in documenting the ability of both parasitoid species to adjust their oviposition schedule (without loss in fecundity) during the 1st 4 d after emergence to adapt to variable host availability.

In addition to periods of deprivation, parasitoids also are likely to experience a range of host densities and spatial patterns. Morrison et al. (1980) found that when *Helicoverpa zea* (Boddie) eggs were densely spaced (a separation distance of 25 cm between eggs), percentage parasitization was inversely density-dependent on egg density. As host eggs were experimentally manipulated to a separation distance of 150 cm, parasitization became density-independent. Klemm and Schmutterer (1993) documented a similar relationship for *T. pretiosum* attacking *P. xylostella*; although more host eggs were parasitized on cabbage plants with high host egg densities, the percentage parasitization actually decreased substantially compared with plants with low densities. In contrast, Gross et al. (1984) documented an increase in the rate of parasitization of *H. zea* on corn with increasing host densities. These variable responses may be in part caused by genetic variability in ovipositional behaviors. Chassain and Boulétreau (1987) determined that some *Trichogramma maidis* Pintureau & Voegelé (now synonymized with *T. brassicae*) females oviposit in an aggregated fashion, whereas others scatter their progeny among distant host eggs. Moreover, a genetic analysis determined that each specific ovipositional behavior was heritable, and stable for at least the 2 generations examined. They suggested that both of these ovipositional behaviors can be evolutionarily justified by the value such diversity brings to adaptation to variable host abundance. The strategy leading to a wider dispersion of parasitoid progeny has been shown for other parasitoids to maximize oviposition rates while minimizing the potential for hyperparasitization (Trumble and Oatman 1984).

If these results can be generalized across species, they have significant implications for using *Trichogramma* spp. in biocontrol efforts. Specifically, inundative releases for rapid suppression of high-density pest populations would be hampered by selection of a genetic type exhibiting a tendency for females to bypass unparasitized eggs near those that were already parasitized.

**Intra- and Interspecific Interference.** Except for using *Trichogramma* spp. in an inundative control program designed for immediate, short-term suppression of an outbreak (i.e., a migratory or generational ovipositional event), competition within and between species for eggs can have a substantial negative effect on the economics of pest control. For many systems, the additional benefit derived from the host-parasitizing activity of offspring from those wasps initially released is economically useful. Because releases often are made monthly or every other week, the emergence of wasps between releases can help suppress pest populations at a time when

oviposition by released adults is declining. This aspect of control programs has not been investigated adequately.

In crops where long-term control is intended, interference between competing females within a species or among different species could be considerable. Studies by Boulétreau et al. (1991) demonstrated that interference between competing females within a species (*T. brassicae*) reduced efficiency of parasitization but that the mutual interference was mitigated if host distributions were patchy. Many researchers have documented substantial reductions in parasitoid quality (longevity, searching ability, etc.) in cases where eggs are superparasitized. Adults emerging from superparasitized eggs tend to be smaller, and smaller females tend to be less fecund (Bai et al. 1992). Roltsch and Mayse (1983) reported on a system where *Trichogramma* spp. and *Copidosoma truncatellum* (Dalman) (an egg-larval parasitoid) were competing for eggs of *Trichoplusia ni* (Hübner). This study suggested that where competition was occurring, the *Trichogramma* spp. parasitization was substantially reduced. Few experimental studies have investigated situations where multiple *Trichogramma* spp. were released. In the most recent report, *T. brassicae* and *Trichogramma cacoeciae* Marchal successfully shared unevenly distributed host resources and avoided multiple parasitization (Boulétreau et al. 1991).

Concurrent or alternating releases of *Trichogramma* spp. and *Chrysoperla carnea* (Stephens) or other egg predators might not be beneficial for long-term development of *Trichogramma* spp. populations. However, the concurrent use of these beneficial insects could be additive or synergistic for short-term efforts; unfortunately, we could find no information on concurrent use in vegetables. However, not all other parasitoid and predator species would necessarily be incompatible. Species attacking the larval stages of the pests (e.g., *Polistes* spp., *Camponotus sonorensis* [Cameron], etc.) should have an additive effect with *Trichogramma* spp. releases.

### Compatibility of Pesticides With *Trichogramma* spp.

**Conventional Chemical Pesticides (Organophosphates, Carbamates, Pyrethroids, etc.).** Information on the effects of conventional chemical pesticides on *Trichogramma* spp. used in vegetable crops is not extensive, but the available studies suggest that although the parasitoids are sensitive to pesticide use, the long-term effects are variable. Jacobs et al. (1984) examined the compatibility between 2 pesticides and *T. pretiosum* released for control of *H. zea* (reported as *Heliothis zea* Boddie) on fresh-market tomatoes and found that residues of the chlorinated hydrocarbon endosulfan had measurable negative effects on adult survivorship and egg parasitization for only 1 d. Similar results were found for the carbamate methomyl (Oatman et al. 1983), where the negative effect was restricted primarily to those *T. pretiosum* immatures and adults present at the time of application. Thus,

an inundative strategy could be compatible with these pesticides if releases were made at least 24 h after pesticide application and if the number of pesticide applications was minimized.

In contrast, residues of the pyrethroid permethrin remained active against *Trichogramma* spp. for at least 21 d on tomatoes (Jacobs et al. 1984) and  $\approx 7$  d on cotton (Bull and House 1983). Esfenvalerate, another pyrethroid, also caused extensive reductions in percentage parasitization by *Trichogramma exiguum* Pinto & Platner and *T. pretiosum* following applications on tomatoes (Campbell et al. 1991). Of the other compounds tested by these authors, methomyl and the organophosphate methyl-parathion were 2 with particularly substantial histories of use on most vegetable crops. Both of these pesticides were found to reduce parasitization rates significantly (70–100%) following repeated applications. Repeated (weekly) applications of methomyl plus carbaryl (Roltsch and Mayse 1983) or methomyl plus fenvalerate (Hoffmann et al. 1990) have also been shown to substantially reduce the percentage parasitization of several *Trichogramma* spp. on a variety of lepidopteran pests of tomatoes.

More recently, Campbell et al. (1991) found that percentage parasitization of *H. zea* on tomatoes by *T. exiguum* and *T. pretiosum* was not significantly different on plants treated repeatedly with endosulfan or methomyl compared with untreated plants. However, possibly because of the disruption of predators, host egg densities were substantially higher in the insecticide treatments; the higher host egg densities were suggested as an explanation for the comparable levels of parasitization.

Limited additional information is available on other pesticides in the literature. A variety of growth regulators (mostly chitin inhibitors) and other pesticides (chlordimeform, thiodicarb, azinphosmethyl, cyhexatin, and some fungicides) has been studied for interactions with a variety of *Trichogramma* spp. on other crops (cotton, castor beans and apples) (Bull and House 1983, Hagley and Laing 1989, Narayana and Babu 1992 and references therein). However, because pesticides have variable effects among crops, extrapolations from these reports to vegetable crops should be made with caution. Nonetheless, the observed compatibility between *Trichogramma* spp. and some of these pesticides does provide suggestions for further research in vegetable crops.

**Biorational Pesticides.** Given the trend for a reduction in the use of pesticides with high mammalian toxicity on many vegetable crops (Trumble 1990), information on the effects of biorational pesticides on parasitoids will become increasingly important. Nonetheless, few detailed reports of investigations on the compatibility of *Trichogramma* spp. and biorational pesticides are currently available.

Klemm and Schmutterer (1993) recently determined the effects of water extracts of neem seeds on *T. pretiosum* and *Trichogramma principium* Sugonjaev & Sorokina in both the laboratory and the field. Topical appli-

cations of neem to host (*P. xylostella*) eggs in the laboratory reduced the number of host eggs parasitized compared with untreated eggs (17.17 versus 33.63 parasitized eggs per female). In a field test with *T. principium*, neem application apparently had little effect on parasitoid activity because numbers of parasitized eggs per plant were slightly higher in the neem treatments than in the controls (99.75 versus 78.0 per plant, respectively). However, an additional study indicated that the neem-treated cabbage also was more attractive to *P. xylostella* for egg laying, with  $\approx 3$  times as many eggs per plant as on the control plants. In a separate test with *T. pretiosum* releases, the neem plots and the control plots had similar levels of parasitization, but percentage parasitization was inadequate to provide an economic level of suppression of the pest. Experiments evaluating host eggs containing *Trichogramma* spp. pupae treated with a formulation of neem oil indicated incompatibility between these control approaches for establishment of long-term control because treated host eggs failed to produce any parasitoids. However, this does not necessarily preclude the use of the wasps in short-term, inundative programs.

New isolates, conjugates, and genetically engineered *Bacillus thuringiensis* variety *kurstaki* Berliner products have appeared rapidly during the past 5–8 years. As a result of the improved efficacy of these products against lepidopterous pests of vegetables, researchers have been stimulated to examine the potential of these materials in integrated pest management programs. Initial reports by Oatman et al. (1983) indicated that *B. thuringiensis* variety *kurstaki* (isolate HD-1) had no adverse effects on *T. pretiosum* attacking *H. zea* in tomatoes. Similar results were reported for *B. thuringiensis* variety *kurstaki* (isolate NRD-12) on fresh-market tomatoes in Mexico (Trumble and Alvarado-Rodriguez 1993). In laboratory tests, Klemm and Schmutterer (1993) found that *B. thuringiensis* variety *kurstaki* (SAN 415, isolate not identified) applied topically to eggs of *P. xylostella* did not significantly reduce the mean number of parasitized eggs per female ( $16 \pm 7.39$ ) compared with water-treated controls ( $20.75 \pm 22.15$ ). Finally, Campbell et al. (1991) found no significant differences between *B. thuringiensis* variety *kurstaki* (isolate HD-1) treatments and the untreated controls in percentage parasitization of *H. zea* and *Heliothis virescens* (F.) eggs by *T. exiguum* and *T. pretiosum* in fresh-market tomatoes. Thus, *B. thuringiensis* variety *kurstaki* appears to have minimal effects on parasitic activity and success of *Trichogramma* spp.

**Antibiotics.** Registration of some antibiotics (primarily streptomycin) for agricultural use has been granted in the United States and other countries (Sine 1993). Streptomycin currently is available for use on vegetables, fruit, and nursery crops for control of a variety of commercially important bacterial diseases. In addition, researchers are investigating the use of other antibiotics (e.g., oxytetracycline) for control of some important vegetable pests, including *Bemisia* spp. and other Homoptera (Sinha and Peterson

1972, Costa et al. 1993). Thus, considerable potential exists for exposure of *Trichogramma* spp. to antibiotic treatments that could have unexpected effects on the viability of *Trichogramma* in long-term biocontrol programs. Interestingly, some species apparently have maternally transmitted microorganisms that confer thelytokous reproduction, and these organisms can be eliminated in the laboratory with antibiotics such as tetracycline, sulfamethoxazole, and rifampicin, causing populations to revert to arrhenotokous reproduction (Stouthamer et al. 1990). As noted previously, this reversion does not decrease the availability of females because arrhenotokous females produce at least as many daughters as their thelytokous counterparts (Stouthamer and Luck 1993). However, further study is desirable because the potential net effect of antibiotics on efficiency of parasitization has not been determined, not all antibiotics tested resulted in arrhenotokous reproduction, and inundative releases with mass-reared thelytokous parasitoids or mixtures of both still might be efficacious.

### Effects of Host Plant Resistance on Effective Use of *Trichogramma* spp.

Although host plant resistance is usually considered to be a viable part of an integrated pest management program for vegetables, considerable evidence is accumulating to indicate that this tactic is not always compatible with biocontrol agents (Obrycki 1986). Plants may be bred for insect resistance using a wide variety of plant characteristics, with both pubescence and allelochemical composition receiving considerable attention (Eigenbrode and Trumble 1994). Several recent studies have provided examples of incompatibility between host plant resistance and *Trichogramma* spp. based on foliar pubescence. For example, Kauffman and Kennedy (1989) found increasing incompatibility with increased pubescence. Regression analyses indicated that trichome density accounted for most of the variance when parasitization rates of *Trichogramma* spp. (*T. pretiosum* and *T. exiguum*) were compared on commercial tomatoes, *Lycopersicon esculentum* (Mill.), susceptible to *Manduca sexta* (L.); the resistant accession, *L. hirsutum* f. *glabratum* C. H. Muller (PI 134417); and a series of backcrosses. Some backcrosses had the type VI glandular trichomes that contain 2-tridecanone and 2-undecanone, which have proven to be toxic to several insect species (Farrar and Kennedy 1987, Lin et al. 1987). Subsequent experiments by Kashyap et al. (1991) determined that *T. pretiosum* could be killed either by direct contact with trichomes containing these chemicals or by exposure to these materials in the volatile state. Even exposure of parasitized eggs to the volatiles dramatically reduced adult emergence rates. Thus, even if eggs were parasitized, the prospects for long-term pest suppression would be minimal with this form of host plant resistance.

Reduced rates of parasitization by *Trichogramma* spp. also were found on tomato plants with high densities of trichomes that did not contain the 2 ketones (Kauffman and Kennedy 1989). In this case, simple physical interference with both movement and normal searching behavior was enough to create an incompatibility between these control strategies. Similar results have been presented for cotton (Treacy et al. 1986), tobacco (Rabb and Bradley 1968), and other crops (Obrycki 1986).

### Semiochemicals That Influence Parasitoid Behavior and Efficiency of Parasitization

In a thorough review of the literature through 1988, Noldus (1989) presented considerable evidence for the presence of semiochemicals from insects and plants that could substantially influence the behavior of a variety of *Trichogramma* spp. Several studies indicated that chemical cues from the presence of moths, moth scales, sex pheromones of the hosts, or exuvia of newly emergent adult moths could elicit positive host-finding responses from *Trichogramma* spp. Some reports even documented an attendant increase in parasitization rate (Noldus 1988, 1989 and references therein). Exposure of parasitoids to plant volatiles induced variable results, with some compounds acting as strong attractants and others repellents (Altieri et al. 1981, 1982; Noldus 1989). Tests to measure such responses to plant odors have yielded conflicting results because these responses can be influenced by previous ovipositional experience (Kaiser et al. 1989).

Since 1988, a series of published studies has attempted to elucidate the mechanisms responsible for alteration of parasitoid behaviors by semiochemicals. Initially, increased parasitization in environments with high levels of host sex pheromones was believed to be caused by long-distance attraction, but more recent studies have suggested an arrestment behavior (Noldus et al. 1990, 1991). *Trichogramma evanescens* (Westwood) parasitizing *Pieris brassicae* (L.) or *Mamestra brassicae* (L.) eggs, and *T. pretiosum* attacking *H. zea* showed increased searching periods, time spent walking, and turning behavior in the presence of host sex pheromones. All of these behaviors could reasonably be expected to increase the probability of encountering a nearby host egg.

Similar behaviors have been demonstrated for contact kairomones associated with host eggs (Wysoki and De Jong 1989, Renou et al. 1992) and host scales (Gardner and van Lenteren 1986, Thomson and Stinner 1990). However, Thomson and Stinner (1990) suggested that even though response to moth scales appeared innate and nonspecific for the 4 species tested, associative learning and conditioning with different host scales might effect variations in the strength of the response. Thus, a case-by-case evaluation for efficacy may be required before making applications of host scales or extracts of scales for retention of parasitoids in inundative release programs

(Gross et al. 1975) or enhancing searching efficiency (Jennings and Jones 1986).

### Case Studies on Tomatoes

Martin et al. (1976) and Oatman and Platner (1971, 1978) provided some of the earliest information on the use of inundative releases of *Trichogramma* spp. in tomatoes. Martin et al. (1976) determined that *T. pretiosum* released at  $\approx 900,000/\text{ha}$  on fresh-market tomatoes in large field cages resulted in 60–70% parasitization of eggs of *H. zea* and *H. virescens*, a level that they considered highly beneficial. However, no data were provided on resulting levels of fruit damage by these pests. Oatman et al.'s (1983) results from using *T. pretiosum* to control *H. zea*, *Manduca* spp., and *T. ni* were particularly encouraging: over a 6-yr period, releases of 1–1.59 million wasps per hectare per season (releases made every other week) suppressed fruit damage by *H. zea* (the primary pest) to  $<5\%$  ( $x = 1.98\%$ ; range, 0.7–4.8%). However, assessing the effect of the releases was difficult because mean damage in control plots was only 3.35% (range, 0.8–5.6%). Nonetheless, they concluded that early-season harvests (by mid-August) of summer plantings benefitted the most from releases, whereas later harvests had essentially equivalent damage levels in both release and control plants. Damage from *Manduca* spp. exceeded 1% in only a single year (maximum 1.6%), and no statistical analyses were conducted. No effort was made in this initial study to determine whether the release rates were economically viable for growers or justified by the level of control. However, at current prices, releasing  $\geq 1$  million wasps per hectare during the season is roughly equivalent to the cost of a pesticide application made to control *H. zea*. At the time that the study was conducted by Oatman et al. (1983), commercial levels of production of *Trichogramma* spp. were considerably less than currently and prices were substantially higher.

In a more sophisticated study, which provided a model of experimental design used by many subsequent researchers, Oatman et al. (1983) compared a commercial standard, IPM, and control treatments. The commercial treatment consisted of weekly applications of methomyl. The IPM approach used weekly applications of *B. thuringiensis* variety *kurstaki* plus twice-weekly applications of *T. pretiosum* totaling 1,235,000 per hectare per season. Although differences in percentage fruit damage were significant ( $P < 0.05$ ) between treatments, damage levels in the IPM and commercial programs were low in 1978 (1.6 and 0.7%, respectively) and 1979 (0.9 and 0.3%, respectively). Under both of these management practices, significantly less damage occurred than with the control treatments, which averaged 7.1% (1978) and 5.3% (1979). In our experience, growers will accept new technologies readily if damage levels are  $<4\text{--}5\%$ . Thus, one might have expected that this approach would have been implemented commer-

cially. However, no economic analysis comparing the IPM and conventional strategies was provided. Given the equivalent numbers of pesticide applications in both programs, similar costs of the pesticides applied (methomyl and *B. thuringiensis* variety *kurstaki*), and the additional costs of purchasing and releasing >1 million wasps per hectare each week, the economics of the IPM program were probably not compelling. Nevertheless, this study was the 1st to demonstrate that an inundative release program combining *B. thuringiensis* variety *kurstaki* with *Trichogramma* spp. could provide commercially acceptable levels of control of *H. zea* on fresh-market tomatoes.

In the 1980s and 1990s, a series of vegetable IPM programs was developed in California and Florida that did not include releases of *Trichogramma* spp. (Schuster et al. 1980, Pohronezny et al. 1986, Toscano et al. 1987, Schuster and Pohronezny 1993). These IPM programs, although covering a variety of pest species, generally focused on pests that could not be controlled by *Trichogramma* spp. In Florida, the overwhelming concern was for leafminer (*Liriomyza* spp.) management. In California, tomato pinworm, *Keiferia lycopersicella* (Walsingham), and *S. exigua* were far more common than *H. zea*, which occurred at mean densities of <0.5 immatures (eggs plus larvae) per 25 plants (Toscano et al. 1987).

More recently, an IPM program was developed for the \$1 billion fresh-market tomato industry in the State of Sinaloa, Mexico (Trumble and Alvarado-Rodriguez 1993). Like the study by Oatman et al. (1983), the research in Mexico in 1988 and 1989 compared an untreated control with a commercial standard treatment (>20 applications of methamidophos + permethrin) and an IPM program. The IPM program consisted of repeated releases of *T. pretiosum* at 100,000/ha per week for a total of 500,000–900,000/ha for *H. zea*, mating disruption for *K. lycopersicella*, and “as needed” applications of *B. thuringiensis* variety *kurstaki* and abamectin for *S. exigua* and *Liriomyza* spp., respectively. Intensive sampling also was integral to the IPM program. The 3 treatments were compared on multiple plantings in the 3 most important tomato producing valleys—Culiacan, Los Mochis and Guasave. Each treatment was replicated 3 times per crop on 0.5-ha plots separated by at least 0.5 km from any other plots. The *T. pretiosum* were released by clipping egg cards (5, per plot, with parasitized *Sitotroga* spp. eggs) to the underside of tomato leaves. This approach probably moderated the potential negative effects of temperature and relative humidity discussed earlier. All pesticides were applied using local practices. To our knowledge, this is one of the first studies on tomatoes to provide a detailed economic analysis documenting potential net profits for growers. The results were encouraging. Despite fewer applications of pesticides under the IPM program, net grower profits were equivalent to those obtained with the commercial standard treatment in the fall crop and were significantly higher in the winter and spring plantings. Much of this advantage

could be attributed to the exceptional levels of resistance to the pesticides used in the commercial treatment (Brewer and Trumble 1991, 1993). Although *T. pretiosum* was released as part of the IPM program (Trumble and Alvarado-Rodriguez 1993), a detailed analysis of the effect of the parasitoids on *H. zea* and *H. virescens* (hereafter called fruitworms) was not included in previous reports. Additional analysis of data collected before and during that study has been completed and is presented here.

Data are available for spring plantings from the Culiacan (1988), Los Mochis (1988 and 1989), and Guasave (1988 and 1989) valleys. Beginning at flowering, groups of 30 leaves per plot were randomly collected within each experimental plot during 1988. The samples were collected from the primary oviposition sites of *H. zea* by selecting the leaf above the highest open flower on the tomato plant (Alvarado-Rodriguez et al. 1982) while crossing the fields in a diagonal pattern, as described by Lange et al. (1985) and Weakly et al. (1986). Most samples contained 10–20 eggs. When numbers of eggs per sample were large (maximum >750 eggs), ≈100 eggs per treatment per week were chosen randomly and processed in the laboratory by placing them into 000-size gelatin capsules and rearing out the parasitoids. Only *T. pretiosum* was reared from these samples.

In Culiacan, where populations of fruitworms were comparatively low, the IPM and control treatments had similar patterns and rates of egg parasitization (Fig. 1). No parasitization was observed in any treatment until the 5th week of sampling, when 25 and 50% of the eggs were parasitized in the control and IPM plots, respectively. Parasitization remained high for another week in these treatments, then declined to 0. No differences in percentage fruit damage by fruitworms were seen between the control and IPM plots; both had economically acceptable levels of damage (mean, 3%). By comparison, parasitization in the commercial standard treatment was minimal, occurring only on a single sample date and reaching only 20% (Fig. 1). However, the pesticides applied for fruitworms were effective because no damaged fruit were found in this treatment (Table 1).

In Los Mochis, fruitworm densities were high in both 1988 and 1989. Again, both the IPM and control treatments had similar temporal patterns of parasitization (Fig. 2a, b). In 1988, the percentage of parasitized eggs fluctuated widely, with the highest rates occurring late in the season. This late-season activity is critical, because fruit were on the plants for only the last 5 wk or so of the spring crop. No parasitization was observed in the corresponding commercial treatment at anytime during the 1988 planting. For 1989, generally higher rates of parasitization occurred. An average of 75–80% of the fruitworm eggs were parasitized in the IPM and control plants during the planting. Parasitization in the commercial standard plots was high early in the season (≈70%, >80% at peak) but declined to 0 for the last 2 wk of sampling.

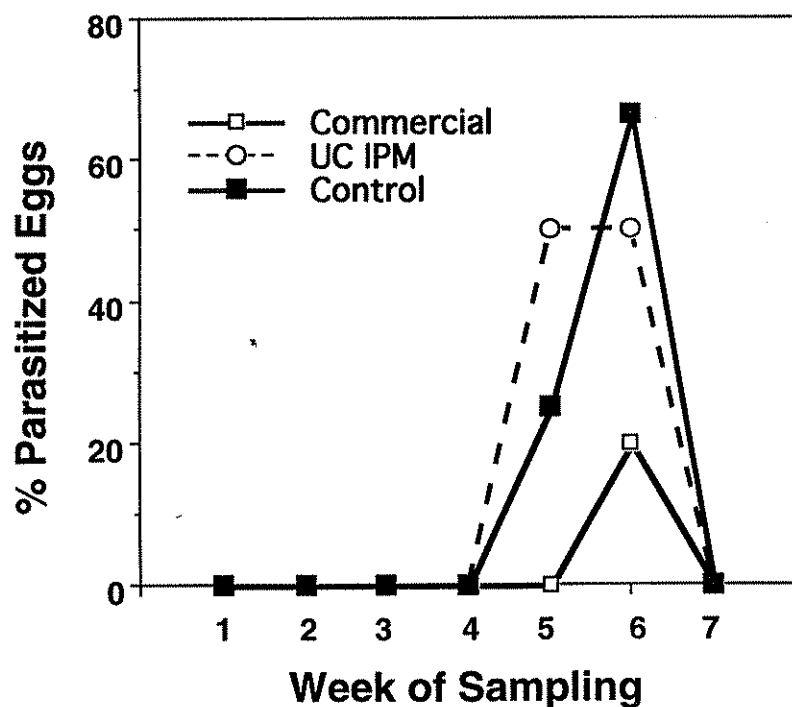


Fig. 1. Percentage parasitization of fruitworm eggs (*H. zea* and *H. virescens*) in commercial, IPM, and control plots during 1988 in Culiacan, Mexico. Parasitization rates based on  $\approx 100$  eggs per treatment per week. Final week of sampling coincided with last date of harvest (week 12 of crop).

Levels of fruit damage from Los Mochis provided some interesting insights into the impact of parasitoids on the fruitworm populations. In spite of similar parasitization rates in 1988 between control and IPM plots, fruitworm damage in the controls was dramatically higher (Table 1). This suggests that applications of abamectin for *K. lycopersicella* and *B. thuringiensis* variety *kurstaki* for *S. exigua* in the IPM program also were efficacious against fruitworms. Thus, as suggested in previous IPM trials by Campbell et al. (1991), the action of the pesticides may have been more important in preventing damage than the control provided by the wasps. This same trend was evident in 1989 when  $>50\%$  more damage occurred in the control planting (Table 1), despite similar rates of parasitization in these treatments.

Populations of fruitworms were variable between 1988 and 1989 in Guasave (Fig. 3a, b). In 1988, when fruitworm populations were relatively low, parasitization in the control and IPM treatments increased rapidly and remained high ( $\approx 80\%$ ) for most of the season. The corresponding com-

Table 1. Percentage fruit damaged by fruitworms (*H. zea* and *H. virescens*) in spring plantings of fresh-market tomatoes in Sinaloa, Mexico

Location	Year	Treatment	% damage <sup>a</sup>
Culiacan	1988	Commercial	0.0
	1988	UC IPM	3.0
	1988	Control	3.0
Los Mochis	1988	Commercial	1.0
	1988	UC IPM	1.0
	1988	Control	29.3
	1989	Commercial	11.5
	1989	UC IPM	6.2
	1989	Control	15.7
Guasave	1988	Commercial	0.0
	1988	UC IPM	0.5
	1988	Control	3.5
	1989	Commercial	8.4
	1989	UC IPM	6.5
	1989	Control	16.4

<sup>a</sup> Damage averaged over all harvests for each crop and weighted by size of harvest.

mercial treatment had low rates of parasitization, reaching 20% on a single sampling date. Fruitworm damage was low in all of these treatments, ranging from 0 to 3.5% (Table 1). In 1989, when fruitworm populations were higher, the percentage parasitization was relatively high for all 3 treatments, including the commercial standard (Fig. 3b). This was the only year and crop in the study where applications of methamidophos + permethrin had a minimal effect on rates of parasitization by *T. pretiosum*. We have no explanation for this effect. While pesticide resistance in the parasitoid population could account for these findings, the lack of equivalent responses from other sites treated similarly suggests that other unknown factors may have been operating.

Regression analyses contrasting fruit damage versus the mean percentage of fruitworm eggs parasitized over the entire season or during the last 3 sampling dates revealed no significant relationships ( $P < 0.05$ ) in the control or IPM treatments. Thus, documenting the precise impact of the parasitoids as opposed to the applications of *B. thuringiensis* variety *kurstaki* or abamectin was not possible in this study. However, the joint effect of these agents resulted in fruitworm suppression that was as economical as the commercial program and environmentally superior.

Given this analysis, it would be easy to assume that the pest suppression provided by the *T. pretiosum* releases was not economically viable. However, this ignores both the low expenses associated with an inundative program in Mexico ( $\approx \$20$  U.S. for 900,000 wasps [Trumble and Alvarado-



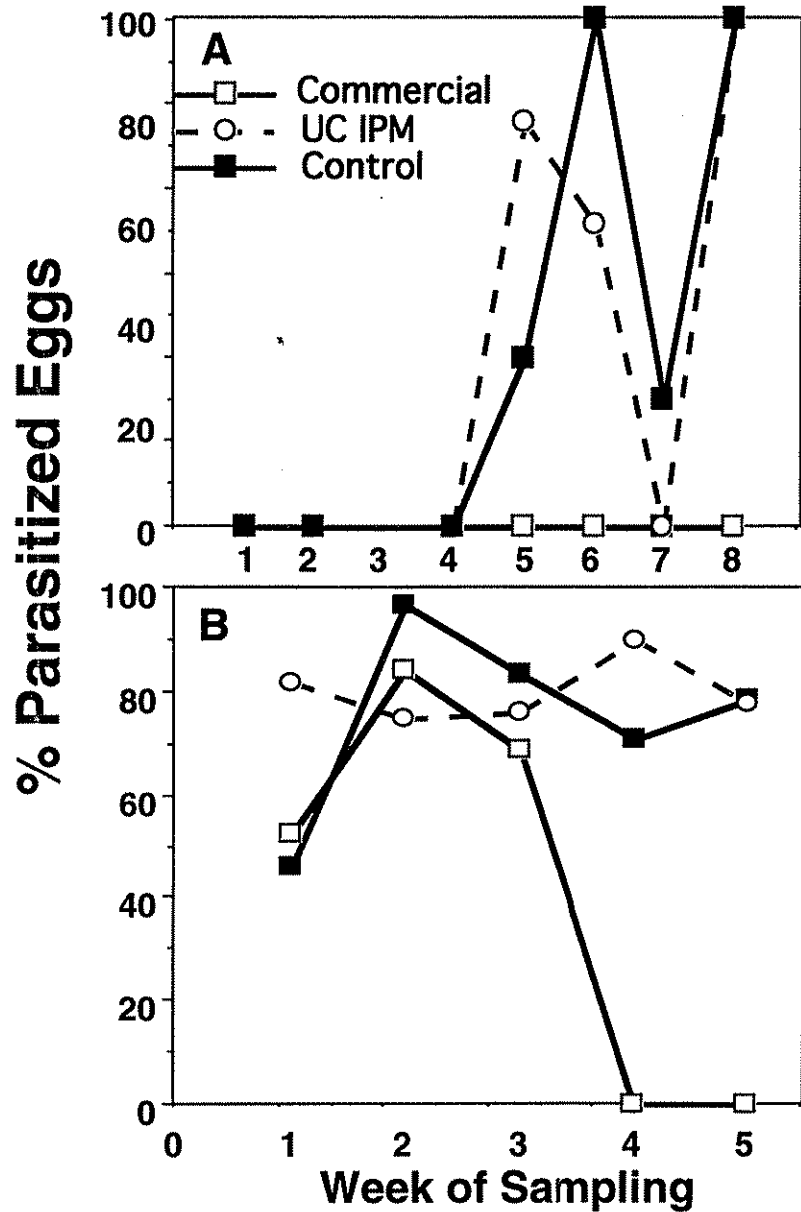


Fig. 2. Percentage parasitization of fruitworm eggs (*H. zea* and *H. virescens*) in commercial, IPM, and control plots during 1988 (A) and 1989 (B) in Los Mochis, Mexico. Parasitization rates based on  $\approx 100$  eggs per treatment per week. Final week of sampling coincided with last date of harvest.

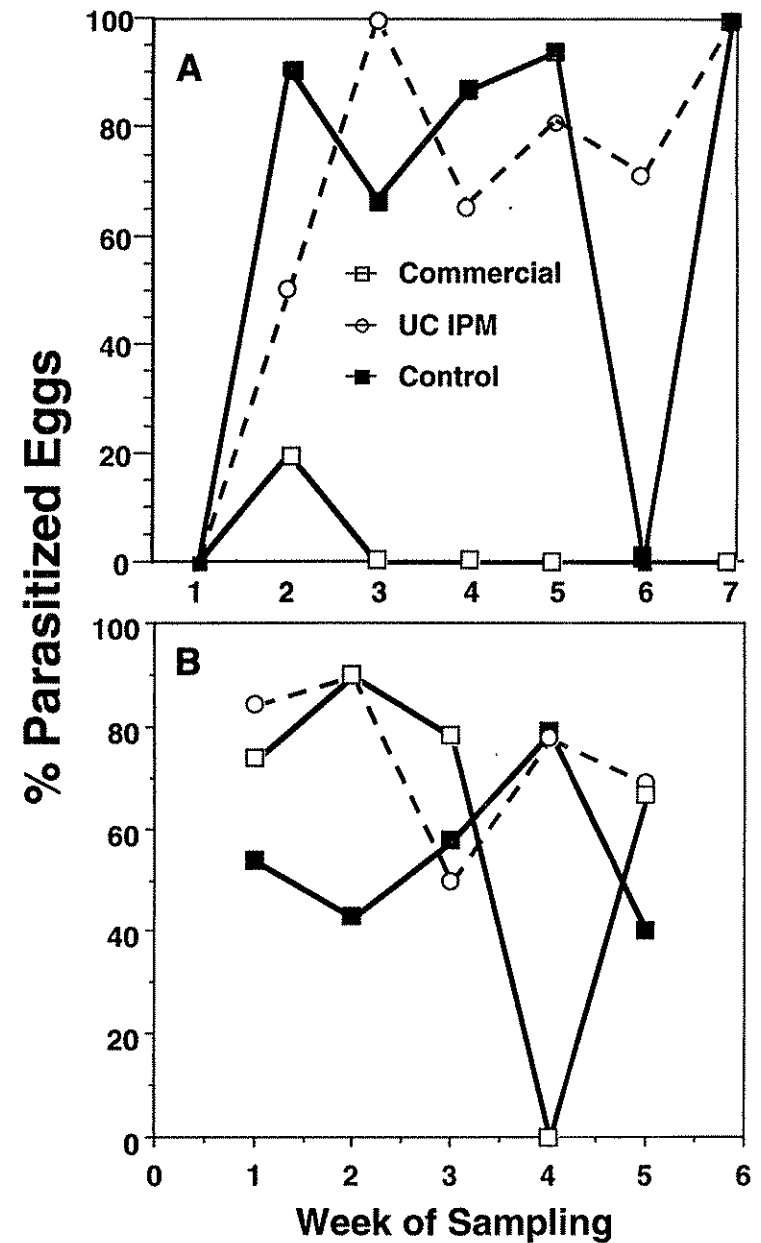


Fig. 3. Percentage parasitization of fruitworm eggs (*H. zea* and *H. virescens*) in commercial, IPM, and control plots during 1988 (A) and 1989 (B) in Guasave, Mexico. Parasitization rates based on  $\approx 100$  eggs per treatment per week. Final week of sampling coincided with last date of harvest.

Rodriguez 1993]), and the potential benefits in resistance management. Parasitization results in a decrease in numbers of survivors that could carry genes for pesticide resistance. Removal of 80–90% of the population, while perhaps not enough to provide commercially acceptable control in every planting, could allow for dilution of resistant genotypes by susceptible migrants, thus slowing resistance development.

Such potential benefits have been recognized by growers of processing tomatoes in Mexico, where a modification of the aforementioned program is currently in use. Adams (1994) and Bolkan and Reinert (1994) reported a 10% decline in fruit damage by *H. zea* in *T. pretiosum*-release fields, even when *B. thuringiensis* variety *kurstaki* was the only pesticide applied. Although the information in these articles was limited (release rates were 750,000/ha, but no details were given on release frequency, statistical significance, etc.), the *H. zea* suppression was considered economically viable, and the growers established their own *T. pretiosum* production facility.

### Conclusions and Prospects

Effective use of *Trichogramma* spp. in commercial vegetable production will be successful only if the ecology of the particular system is thoroughly understood. Problems with environmental factors, strain selection, and quality control, as well as incompatibility with some pesticides and some forms of host plant resistance, will reduce the probability that this strategy can consistently replace or augment pesticides. In time, additional research may furnish enough answers so that we can consistently maximize pest control with these wasps and eliminate or greatly reduce pesticide use. However, recognizing the value of partial success (i.e., significant, but not economical pest suppression) in IPM programs is likely to become increasingly important. The pest population reductions provided by such partial successes may not only allow use of less toxic pesticides and more effective use of semiochemical techniques and new varietal introductions, but can help minimize development of pest resistance to insecticides.

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