

Comparison of *Trichogramma brassicae* (Hymenoptera: Trichogrammatidae) Augmentation with Organic and Synthetic Pesticides for Control of Cruciferous Lepidoptera

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Environ. Entomol. 31(6): 1231–1239 (2002)

ABSTRACT We monitored egg parasitism and larval populations of *Pieris rapae* (L.) and *Trichoplusia ni* (Hübner) in cabbage plots treated with point and broadcast releases of *Trichogramma brassicae* Bezdenko, and we investigated whether weekly sugar sprays improved egg parasitism rates. We also compared yield and pest densities in cabbage treated with *Bacillus thuringiensis* (Dipel), methomyl (Lannate), or point releases of *T. brassicae* to an untreated control, and investigated the economics of these control strategies. Egg parasitism was highest in the point release treatment (46%), and parasitism in the broadcast and the broadcast + sugar spray treatments (31 and 24%, respectively) did not differ from the control. Weekly applications of sucrose did not increase egg parasitism or decrease larval pest populations. Releases of *T. brassicae* did not significantly reduce *P. rapae* and *T. ni* larval populations, and plant damage and cabbage head weight were unaffected in the *T. brassicae* treatments relative to the control. In addition, the cost of applying the *T. brassicae* wasps was not recouped with significant yield improvements relative to the control. Methomyl and *Bt* consistently suppressed *P. rapae* and *T. ni* populations below action thresholds in a cost-effective manner.

KEY WORDS *Bacillus thuringiensis*, biological control, cabbage, *Pieris rapae*, sugar sprays

CONTROL OF *Pieris rapae* (L.), the imported cabbage-worm, and *Trichoplusia ni* (Hübner) the cabbage looper, in cabbage consists primarily of insecticide sprays (Subramanyam et al. 1996, NASS 1998). Reasons for the reliance on pesticides include a low tolerance for plant damage in fresh market produce (Shelton et al. 1982) and the inability of endemic natural enemies to reliably reduce *P. rapae* and *T. ni* densities to acceptable levels (Parker 1970, Weires and Chiang 1973). The importance of insecticides to cabbage production is undeniable; however, the list of adverse effects on human health and the environment resulting from some pesticides continues to grow (Pimentel et al. 1993), and a more integrated approach to pest control that reduces the use of insecticides incorporating alternative pest control strategies is being sought for all cropping systems (FQPA 1997, GAO 2001). Development of an augmentation biological control program that increases the numbers of natural enemies in cabbage fields may help to reduce the reliance on insecticides within the cabbage system.

There is little or no egg parasitism of *P. rapae* or *T. ni* in the north-central United States (Harcourt 1962, Weires and Chiang 1973). Scientists from North

America and Europe have attempted to exploit this empty niche with generalist egg parasitoids in the genus *Trichogramma* (Oatman et al. 1968, Parker and Pinnell 1972, Oatman and Platner 1972, van Lenteren and Pak 1984, Pak et al. 1989). *Trichogramma evanescens* Westwood is the only species that has been reared from field-collected *P. rapae* eggs in Europe (van Lenteren and Pak 1984), and has been the only species of *Trichogramma* to effectively reduce *P. rapae* populations to acceptable levels in North America (Parker et al. 1971, Parker and Pinnell 1972).

A number of *Trichogramma* spp. use *T. ni* eggs as hosts, and this pest has been used as a factitious host for culturing *Trichogramma* in the laboratory (Oatman and Platner 1972, Hohmann et al. 1988, Kazmer and Luck 1995). Unfortunately, the taxonomy of *Trichogramma* has been resolved only recently, and many of the species used in research before the 1990s were misidentified, and voucher specimens are scarce. For instance, *T. evanescens* used in research conducted by Parker et al. (1971) and Parker and Pinnell (1972) that led to successful suppression of *P. rapae* and *T. ni* may actually have been a strain of *Trichogramma brassicae* Bezdenko (Pinto 1998). To further complicate the application of past research, intraspecific strains of *Trichogramma* display a wide range of behavioral variation that may render certain strains ineffective as control agents (Pak and van Heiningen 1985,

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van Dijken et al. 1986, Pak and De Jong 1987, Pak et al. 1989, Hegazi et al. 2000). Thus, new strains of previously successful *Trichogramma* spp. cannot be assumed to produce the same level of pest control as their predecessors.

Despite the questions concerning past research, the success of *Trichogramma* spp. in cabbage and other systems is well documented (Smith 1996). Moreover, *Trichogramma* are relatively easy and affordable to mass-produce, and these egg parasitoids kill their hosts before the pest hatches and begins to damage plants. For these reasons, the development of a commercially produced strain of *Trichogramma* that can control cruciferous Lepidoptera is appealing.

Methods for releasing *Trichogramma* spp. are a critical component of a pest control program (Stern et al. 1965, Keller et al. 1985, Smith 1994). In general, ground applications of *Trichogramma* can be categorized as either "broadcast releases" or "releases from point sources" (Smith 1994). Point releases of *Trichogramma* involve placing a number of parasitized hosts or recently emerged adult wasps at one or more fixed sites in an agricultural area. This method temporarily protects the released parasitoids from environmental factors and predation, but relies on the wasps to disperse and parasitize hosts evenly throughout the field, a phenomenon that is idiosyncratic and potentially unreliable (Hendricks 1967, Keller et al. 1985, Losey et al. 1995). Broadcasting *Trichogramma* evenly distributes parasitized hosts throughout an agricultural area at the expense of the protective benefits afforded by the point release sites. Both methods are commonly used under different circumstances, although we were unable to find any published reports of direct comparisons between point and broadcast release methods.

Agroecosystems are often devoid of food sources that sustain populations of biological control agents, and once introduced, these agents either die or disperse in search of resources before parasitizing all of the available hosts. One food source used by *Trichogramma* spp. is sugar, which is available in the field in the form of honeydew and nectar (Hagen 1986, Evans 1994). Providing sucrose to *Trichogramma* in the laboratory has consistently been shown to increase adult longevity (Hohmann et al. 1988, Leatemia et al. 1995, McDougall and Mills 1997, Lundgren and Heimpel 2002b), and *Trichogramma* inflicts higher rates of field parasitism in cotton that has extra-floral nectaries relative to nectariless cotton (Treacy et al. 1987). In other cropping systems, artificial food sources have been provided as attractants to natural enemies (Carlson and Chiang 1973, Ben Saad and Bishop 1976a, Hagen et al. 1976, Evans and Swallow 1993), and this strategy has in some cases led to improvements in pest control (Schieffelin and Chiang 1966, Ben Saad and Bishop 1976b, Baggen and Gurr 1998, Cañas and O'Neil 1998). To date, the role of sugar sprays in conserving *Trichogramma* wasps in augmentation biological control programs has not been examined.

Here, we evaluated the potential of a commercially produced strain of *T. brassicae* to control *P. rapae* and *T. ni* in cabbage fields. We compared parasitism rates and pest mortality after point and broadcast releases of *T. brassicae* and evaluated the ability of weekly sugar sprays to improve egg parasitism rates. We also compared yield, pest reduction, and the cost of pest management in cabbage treated with *Bacillus thuringiensis* (Dipel, used in organic cabbage production), methomyl (Lannate, a carbamate that is approved for use against cabbage pests), or point releases of *T. brassicae*.

Materials and Methods

Study Site. Research was conducted at the University of Minnesota Experiment Station in Rosemount, MN. Cabbage (*Brassica oleracea* var. *capitata* L., 'Gourmet') was transplanted on 22 June 1999 with seedlings provided by Speedling Inc. (Bushnell, FL) and on 27 June 2000 with seedlings provided by a local grower. A preplant incorporated herbicide, Treflan (Dow AgroSciences, Indianapolis, IN), was applied at label rates. After planting, weeds were manually removed from the plots as needed. Water was applied during dry periods, and anhydrous ammonia was applied twice during the 2000 season.

In both years, four treatments with four replicates each were arranged in a complete randomized design and embedded in a 4.05-ha field of soybeans. Each plot had ≈ 250 cabbage plants in eight rows of ≈ 31 plants. Row spacing within plots was 1 m, and plant spacing within rows was 0.39 m. Dimensions for each plot were 9.3×12.5 m. There was 48 m between plots north to south and 20 m between plots east to west.

Treatments. In 1999, we compared the ability of point releases of *T. brassicae* to control pests relative to pesticides used in conventional and organic systems. The four treatments were applications of *Bt* (Dipel DF; Abbott Laboratories, North Chicago, IL), methomyl (Lannate LV; DuPont Agricultural Products, Wilmington, DE), *T. brassicae* released at point release sites, and an untreated control. In 2000, we evaluated the relative pest control capabilities of point releases of *T. brassicae*, broadcast releases of *T. brassicae*, broadcast releases of *T. brassicae* coupled with weekly sugar sprays, and an untreated control.

Insecticide applications in 1999 were made based on thresholds involving cabbage looper equivalents (CLEs) (Shelton et al. 1982) in which one CLE is equivalent to one *T. ni* larva or 1.5 *P. rapae* larvae. Treatment thresholds were three CLEs per 10 pre-heading plants and one CLE per 10 heading plants. Diamondback moth, *Plutella xylostella* (L.), did not reach pest status during this research (JGL and GEH, unpublished data) and was not evaluated in this study. Decisions to apply pesticides were made independently for each replicate of the two insecticide treatments. Consequently, the number and timing of applications made varied among the replicates of these two treatments. *Bt* was applied at 1.12 kg/ha, and methomyl was applied at 3.51 liter/ha within 24 h of

the thresholds being breached using a CO₂ sprayer (2.04 kg/cm²). The adjuvants *Silwet* L-77 and LI-700 (Loveland Industries, Greeley, CO) were added to the pesticide mixtures at 1 liter per 49.8 liters of pesticides and 1 liter per 25.14 liters, respectively, to increase the persistence of the insecticides.

T. brassicae were received weekly from Beneficial Insectary (Oak Run, CA). Weekly shipments of ≈82,000 parasitized *Ephestia kuhniella* Zeller eggs were released after 6 August 1999 and 14 July 2000 as parasitized eggs affixed to cards in the point release treatment and loose parasitized eggs in the broadcast treatments. Parasitized eggs for all treatments originated from the same stock at the insectary. Parasitized eggs were stored at room temperature and were released before 0900 h on the first day of wasp emergence. Mean ± SEM daily temperatures on release dates were 21.18 ± 0.37°C in 1999, and 21.22 ± 0.77°C in 2000; rainfall never exceeded 0.03 cm on release days. To assess the quality of each shipment of *T. brassicae*, two release cards and two groups of >1,000 loose parasitized *E. kuhniella* eggs were deposited into individual 36-ml vials and placed in the field until emergence. The proportion of wasps that were male was calculated for each shipment by viewing antennal setation and genitalia at 50×. The mean ± SEM proportion of released wasps that were male was 0.49 ± 0.01 in 1999 and 0.44 ± 0.01 in 2000. Wasp emergence was verified for each release. Voucher specimens identified by John Pinto (Department of Entomology, University of California, Riverside) were deposited with the Insect Museum at the Illinois Natural History Survey.

For the point release evaluation, the cards with parasitized eggs were separated into 60 release cards (≈5,400 parasitized eggs each). Each release card was placed into a 0.24-liter glass jar with a screen top (1 mm² mesh size). A 70-mm diam piece of filter paper was placed over the top of the screen until the release to prevent wasp escape (Heimpel et al. 1999). Fourteen jars were placed at fixed release sites within each plot beneath "*Trichogramma* houses," inverted Styrofoam bowls suspended by three plastic forks. The 14 release sites were evenly distributed within the plots and remained the same throughout the summer.

For the broadcast release evaluation, the total mass of the eggs, which represented an estimated 668,000 parasitized eggs, was divided into eight parts; and one part was released in each replicate of the broadcast release and broadcast release + sugar spray treatments. Each release consisted of 1.12 ± 0.02 g of eggs per replicate plot. Groups of parasitized eggs were kept individually in 35 × 10 mm petri dishes until wasp emergence. With the onset of wasp emergence, the unemerged parasitized eggs were poured into a saltshaker that had all but one of its holes blocked. In a broadcast release or broadcast release + sugar spray plot, each plant received a single shake of parasitized eggs (334.4 ± 40.7; *n* = 8). Thus, approximately the same number of parasitized eggs was released per plot and on the same days in the point and broadcast release treatments. In the release + sugar spray treat-

ment, sugar was applied once weekly directly after the release of *T. brassicae*. Sucrose was applied at 64.5 kg/ha with a CO₂ sprayer (2.04 kg/cm²). This corresponds to 180 g of sugar per 2-liter bottle of water, or an 8% sucrose solution by weight.

Field Sampling. Plots were sampled up to three times each week, and sampling began 2–3 wk after cabbage transplantation. Five randomly selected plants were sampled per plot in 1999. Ten plants per plot were sampled before 17 August 2000, and seven plants after 17 August 2000. The numbers of *P. rapae* and *T. ni* larvae were recorded for each sampled plant in 1999 and 2000, and the total number of pest eggs per sampled plant was recorded in 2000. On each sampling date in 1999 and 2000, a maximum of five *P. rapae* and *T. ni* eggs per plant were removed with a 12-mm diam cork borer and placed into a plastic petri dish. All insects collected in the point release plots were segregated by plant and plot of origin. In the point release treatment in 2000, the distance from each sampled plant to the nearest release point was measured to the nearest centimeter. Eggs were brought back to the laboratory, excess cabbage foliage was removed from around the eggs, and eggs were placed in 1.5-ml microcentrifuge tubes until they hatched or parasitoids emerged. All specimens were reared on a laboratory bench at ≈22°C and 40% RH.

1999 Harvest Data. Ten cabbage heads per plot were randomly selected and harvested on 27 August and 3 September 1999. Heads with their loose outside leaves ("wrapper leaves") removed were weighed to the nearest 0.023 kg and subjected to the following rating scale, derived from Greene et al. (1969): (1) no insect damage; (2) estimated 0–1% leaf area on the plant with insect damage, no head damage; (3) estimated 1–10% leaf area on the plant with insect damage, no head damage; (4) estimated >10% leaf area on the plant with insect damage, no head damage; (5) as in 4, but with 1–10% head area with insect damage, only to outer layer of leaves; (6) estimated >10% head area with insect damage penetrating several layers of leaves.

1999 Economic Treatment Evaluation. Seasonal cost of treatment was calculated based on the price of the insecticides at the beginning of the 1999 season plus an application fee of \$4 per treatment. The cost of the *T. brassicae* included shipping and handling. The mean number of applications per treatment was calculated for the insecticide treatments, and there were eight theoretical *T. brassicae* releases, which corresponds to the 8 wk of the season after pest eggs were first detected.

The gain threshold, the number of heads per plot that must be rescued to justify treatment (Pedigo 1989), was calculated for each treatment in the following manner. A market value of \$10/22.68 kg of cabbage (or \$0.40 for each cabbage head) was estimated from the Chicago Wholesale Fruit and Vegetable Report (<http://www.ams.usda.gov/fv/mncs/hxw.pdf>). It is important to note that *T. brassicae* and *Bt* are organically certified treatments and organically produced cabbage demands a higher financial return;

the higher market value for organic crops was not considered in this analysis. In the *T. brassicae* analysis, only half of the seasonal treatment cost was used to calculate the gain threshold because wasps were released four times in 1999. Heads with damage ratings <5 were considered marketable, and the proportion of marketable heads was estimated for each replicate plot and compared with analysis of variance (ANOVA) and the Tukey-Kramer means comparison. The mean number of marketable heads per plot was determined by multiplying the mean proportion of marketable heads by 250 (the number of plants per plot). The number of heads rescued per treatment was calculated by subtracting the number of marketable heads in the control treatment from the number of marketable heads in each of the experimental treatments.

Data Analysis. Egg parasitism was defined as the number of eggs that yielded *T. brassicae* adults divided by the number of eggs that yielded either pest larvae or *T. brassicae* adults. In 2000, the egg parasitism rates were compared among the four treatments using a repeated measures ANOVA, and the Tukey-Kramer means comparison was used to reveal specific significant relationships among the treatments. Within the point release plots in 2000, the distances to the nearest release sites were compared with the rates of *P. rapae* egg parasitism by linear regression, pooled over sample dates. The correlation between mean density of *P. rapae* eggs per plot and mean parasitism rate per plot on each sampling date for each treatment was estimated using linear regression.

In 1999, direct comparisons of pest control between the pesticide treatments and the *T. brassicae* point releases were not possible because *T. brassicae* was only released after 6 August, and pesticides were applied throughout the season. However, the mean numbers of pest larvae per plant were compared among the pesticide treatments and the control using a repeated measures ANOVA, and the Tukey-Kramer means comparison was implemented to reveal specific significant relationships among the treatments pooled over all dates. Also in 1999, the number of pest larvae per plant after 6 August was compared between the *T. brassicae* treatment and the control with a repeated measures ANOVA. In 2000, the mean number of *P. rapae* and *T. ni* larvae per plant was compared among the treatments with a repeated-measures ANOVA.

In 1999, the mean head mass and mean damage rating were calculated for each replicate plot. The treatment means for these parameters were then compared among the insecticide treatments and the control with ANOVA and a Tukey-Kramer means comparison. The mean head weight and damage rating for the *T. brassicae* treatment were compared with the control using a *t*-test; this treatment was not analyzed with the insecticide treatments because the plots in the *T. brassicae* treatment were only treated for half the season. The number of pest control applications and the seasonal application costs were compared among the *T. brassicae* and pesticide treatments using ANOVA and Tukey-Kramer means comparisons.

Table 1. Mean \pm SEM egg parasitism rates for *Pieris rapae* in cabbage plots treated with *Trichogramma brassicae* applied with different release procedures in 1999 and 2000

Year	Treatment	Proportion parasitized
1999	Control	0
	Point release	0.19 \pm 0.04
2000	Control	0.15 \pm 0.027b
	Point release	0.46 \pm 0.040a
	Broadcast	0.31 \pm 0.037ab
	Release + sugar spray	0.24 \pm 0.041ab

All sample dates were pooled for each mean. No inferential tests were applied to the means presented for 1999 treatments, and means among the four treatments in 2000 were compared with the Tukey-Kramer means comparison ($\alpha = 0.05$). Means followed by different letters are significantly different.

Results

Egg Parasitism. In 1999, egg parasitism was only detected in the point release treatment, and mean egg parasitism after pooling the sampling dates was 19% (Table 1). In 2000, there was a significant effect of treatment on egg parasitism rates ($F_{3, 12} = 7.368$, $P = 0.005$), and egg parasitism by *T. brassicae* was observed in the control plots (Table 1). The seasonal mean parasitism rate was significantly different among treatments ($F_{3, 12} = 6.97$, $P = 0.006$), and the point release had significantly higher rates of parasitism than the control (Table 1). Parasitism rates in the two broadcast treatments did not differ significantly from the control (Table 1). In the point release plots of 2000, there was no correlation between egg parasitism and proximity to the release sites ($r^2 = 0.006$, $F_{1, 199} = 1.27$, $P = 0.26$). There was no relationship between parasitism and host density in any of the treatments when analyzed individually (point release: $r^2 = 0.008$, $F_{1, 60} = 0.50$, $P = 0.48$; release + sugar spray: $r^2 = 0.018$, $F_{1, 59} = 1.10$, $P = 0.30$; broadcast: $r^2 = 0.001$, $F_{1, 63} = 0.09$, $P = 0.76$).

Pest Populations. Methomyl and *Bt* maintained *P. rapae* and *T. ni* larvae below economic thresholds, and both treatments significantly reduced the number of pests per plant relative to the control ($F_{2, 9} = 134.08$, $P < 0.001$; Fig. 1). *P. rapae* egg populations were largest in early August 2000 (Fig. 2). *T. ni* egg populations were <0.3 eggs per plant in both years. The number of pest eggs per plant throughout the 1999 season was comparable to the seasonal densities observed on large-diameter plants in 2000. Releases of *T. brassicae* did not reduce larval populations in 1999 ($F_{1, 6} = 2.31$, $P = 0.18$) or 2000 ($F_{3, 12} = 4.34$, $P = 0.732$). There were 10 *P. rapae* and *T. ni* larvae per plant when *T. brassicae* releases were begun in 1999 (Fig. 1), whereas there was <1 larva per plant when releases were begun in 2000, and the populations never exceeded 7 larvae per plant in any of the 2000 plots.

Harvest Data. Head weight and plant damage did not differ between the *T. brassicae* point release treatment and the control (head weight: $t = 1.33$, $df = 6$, $P = 0.23$; damage rating: $t = -0.137$, $df = 6$, $P = 0.895$; Table 2), but damage was significantly lower in the insecticide treatments relative to the control ($F_{2, 9} =$

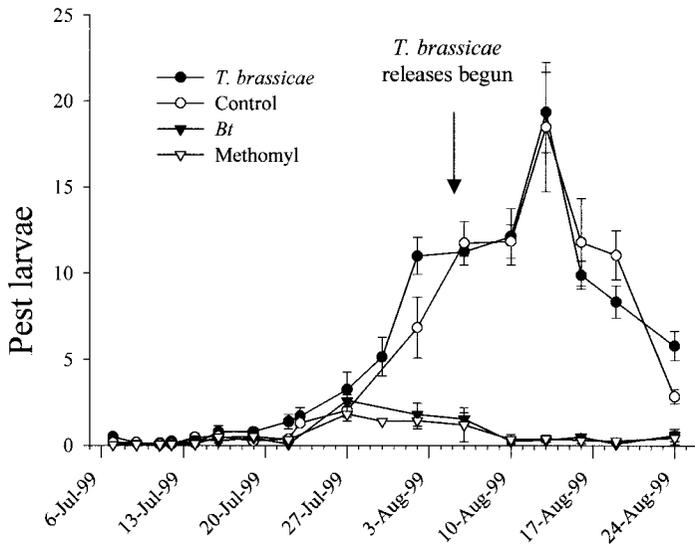


Fig. 1. Mean \pm SEM number of *Pieris rapae* and *Trichoplusia ni* larvae per plant in cabbage plots treated with different pest management options in 1999 ($n = 4$ for each treatment on each sample date). *Trichogramma brassicae* applications were released weekly after 6 August 1999.

340.34, $P < 0.001$; Table 2). Cabbage head weights in the methomyl treatment were significantly higher than head weights in the control plots ($F_{2,9} = 7.88, P = 0.01$; Table 2).

Cost Analysis. A significantly lower number of methomyl treatments were necessary to suppress pest larvae relative to the *T. brassicae* treatment (when applied on a weekly schedule) ($F_{2,9} = 15.8, P = 0.001$), and the cost of individual treatments for *T. brassicae* was higher than for methomyl or *Bt* ($F_{2,9} = 581.33, P < 0.001$; Table 3). These circumstances result in a significantly higher treatment cost for *T. brassicae* than either of the insecticide options (Table 3). The num-

ber of heads rescued by pest control applications exceeded the gain thresholds in the insecticide treatments, but not in the *T. brassicae* treatment (Table 3). Also, the number of marketable heads in the insecticide treatments was significantly higher than the control and *T. brassicae* treatments ($F_{3,12} = 186.12, P < 0.001$; Table 3). The estimated number of heads per plot rescued by *T. brassicae* was 12.5 ± 15.31 , but the total number of marketable heads in the *T. brassicae* treatment was not significantly different from the number of marketable heads in the control (Tukey-Kramer means comparison, $\alpha = 0.05$).

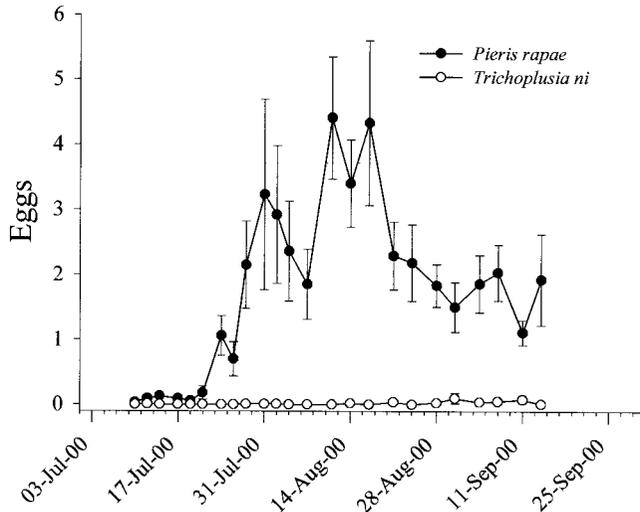


Fig. 2. Mean \pm SEM abundances of *P. rapae* and *T. ni* eggs per cabbage plant in 2000 ($n = 16$ for each species on each sample date).

Table 2. Mean \pm SEM damage levels and cabbage head weights for cabbage plants in plots treated for *P. rapae* and *T. ni* with different pest management tools in 1999

Treatment	Damage rating	Head weight, kg
Control	5.36 \pm 0.08b	1.65 \pm 0.14b
<i>Bt</i>	1.91 \pm 0.33a	2.01 \pm 0.41ab
Methomyl	1.99 \pm 0.03a	2.42 \pm 0.20a
<i>T. brassicae</i>	5.19 \pm 0.21	1.69 \pm 0.58

Mean damage ratings and head masses were compared among the *Bt*, methomyl, and control treatments ($n = 4$ for each treatment) with a Tukey-Kramer means comparison ($\alpha = 0.05$); and the damage rating and head mass in the *T. brassicae* treatment was compared with those of the control using a *t*-test. Values in columns followed by different letters are significantly different. Values in the *T. brassicae* treatment did not differ from the control.

Discussion

We conclude that the commercially produced *T. brassicae* strain evaluated in this research is not an acceptable control agent for cruciferous Lepidoptera. *T. brassicae* was unable to reduce *P. rapae* or *T. ni* larval populations in 1999 or 2000, despite a maximum egg parasitism rate of 46% for *P. rapae*. Egg parasitism was highest in the point release treatment, possibly because *T. brassicae* dispersed evenly throughout the small plots used in this experiment and because the *Trichogramma* houses may have offered some protection from mortality factors. Sugar sprays did not increase the egg parasitism or reduce *P. rapae* or *T. ni* larval populations relative to the unsprayed release treatment or the control. Several factors may have contributed to the low egg parasitism rates observed in our study, including host selection and foraging behaviors of the commercially available *T. brassicae* strain, and the disappearance, resulting from mortality and/or dispersal, of wasps before they could parasitize all of the available hosts. Finally, the *Bt* and methomyl treatments reliably reduced pest populations below action thresholds and resulted in yield improvements that recouped the cost of treatment.

Selection of the optimal species and strain for a particular system is regarded as the first step in a successful biological control program using *Trichogramma* spp. In our study, egg parasitism was <50% despite the broad availability of hosts, and *T. brassicae* did not increase the rate of egg parasitism in response to increases in host egg density in any of the treatments. Host recognition varies between *Tri-*

chogramma strains (Pak and De Jong 1987, Nasr and Shonouda 1998), and there may be alternative species or strains of *Trichogramma* that are more appropriate parasitoids of *P. rapae* and *T. ni* in the cabbage system. Nevertheless, parasitism of *P. rapae* eggs by the commercially produced strain of *T. brassicae* was observed in all of the treatments, although it did not result in significant reductions of pest larvae. Life table analyses of *P. rapae* and *T. ni* would be useful in determining how many eggs must be destroyed before larval populations are reduced to acceptable levels.

Trichogramma mortality may result from host incompatibility, predation of wasps and parasitized host eggs, and adverse environmental conditions. As shown in this research, *T. brassicae* is able to complete development in *P. rapae* eggs, though it is possible that a portion of the *P. rapae* population was able to arrest the development of *T. brassicae* (Lundgren and Heimpel 2002a). If there is physiological resistance in a portion of the *P. rapae* population, then higher rates of egg parasitism may be unattainable with this strain of *T. brassicae*.

Trichogramma mortality through predation on parasitized eggs is well documented (Parker et al. 1971, Lingren and Wolfenbarger 1976, Yu and Byers 1994, Suh et al. 2000), and although we were unable to find any documentation of predation on adult *Trichogramma*, other parasitoids of this size can suffer heavy predation in the field (Heimpel et al. 1997, Rosenheim 1998). In an inundative biological control program, where perpetuation of the agent over multiple generations is not the goal, predation on parasitized hosts is not as detrimental to the program as predation on adults that are capable of inflicting pest mortality. Further research into predation on adult wasps might enable us to adjust release rates to compensate for this mortality factor.

Finally, abiotic environmental factors such as temperature (Parker et al. 1971, Pak and van Heiningen 1985, Chihrane and Lauge 1996, Orr et al. 1997), rainfall, and humidity can all impact *Trichogramma* mortality and performance (see Keller et al. 1985 for review). Climatic conditions in our study were not consistently extreme, though the climatic preferences of this strain of *T. brassicae* are untested, and we don't know how these abiotic factors may have affected field parasitism.

Table 3. Economic comparisons among pest management options used for control of *Pieris rapae* and *Trichoplusia ni*

Treatment	Mean no. applications ^a	Seasonal application cost per replicate	Gain threshold ^b	No. marketable heads	Estimated no. heads rescued by treatment
<i>T. brassicae</i>	8b	\$86.80c	108.5	25 \pm 15.31a	12.5 \pm 15.31a
Methomyl	5.5 \pm 0.29a	\$24.37 \pm 1.28a	60.91 \pm 3.20	240.63 \pm 3.13b	228.13 \pm 3.13b
<i>Bt</i>	7.25 \pm 0.48b	\$31.68 \pm 2.09b	79.21 \pm 5.23	237.5 \pm 8.84b	225 \pm 8.84b

Values are mean \pm SEM, and values within columns that have different letters are significantly different (Tukey-Kramer means comparison, $\alpha = 0.05$). There were four replicates in each treatment.

^a Units are number of releases in the *T. brassicae* treatment, and number of sprays for the insecticide treatments.

^b Gain threshold is defined as the number of preserved cabbage heads required to recoup the cost of the treatment.

Dispersal of *Trichogramma* is a commonly observed phenomenon (Stern et al. 1965, Andow and Prokrym 1991, Greatti and Zandigiacomo 1995, Bigler et al. 1997, Wright et al. 2001) and is likely to have occurred in and among our plots. Wind has important effects on *Trichogramma* dispersal (Hendricks 1967, Yu et al. 1984, Fournier and Boivin 2000) and may be responsible for blowing the wasps out of agricultural plots. The low canopy of cabbage may promote the dispersal of *Trichogramma* out of plots because there is little wind obstruction, and wasps that make short dispersal jumps are likely to be carried out of plots (Keller et al. 1985, Fournier and Boivin 2000).

The provision of food in the form of sugar increases *Trichogramma* longevity and fecundity in the laboratory (Hohmann et al. 1988, Leatemia et al. 1995, McDougall and Mills 1997, Olson and Andow 1998), and theoretically should improve biological control (Hagen 1986, Evans 1994, Jervis et al. 1996; Gurr and Wratten 1999). It is apparent that *Trichogramma* spp. can benefit from food sources in the field because pest control by *Trichogramma* has been increased in cotton with extra-floral nectaries relative to nectariless cotton (Treacy et al. 1987), and honey-fed *Trichogramma minutum* Riley parasitized more hosts in field cages than did starved *T. minutum* over a 4-d period (Smith et al. 1986). Furthermore, parasitism by other minute parasitoids has been promoted by intercropping with plants that have floral nectar (Jervis et al. 1996, Baggen and Gurr 1998). It is difficult to explain why sugar sprays did not enhance parasitism by *T. brassicae* within our plots. It may be that *T. brassicae* cannot consume sugar once it has dried (but see Bartlett 1962), that weekly sprays are not frequent enough to improve *T. brassicae* fitness in the field, or that the increased number of predators observed in the sugar spray plots (JGL, unpublished data) increased mortality of *T. brassicae*.

The high cost of *Trichogramma* relative to insecticides is neither a new or insurmountable problem. *Trichogramma* can be used cost-effectively in high-value crops such as seed corn and possibly sweet corn (Andow 1997), and there are benefits to using *Trichogramma* that are not apparent in direct economic comparisons between *Trichogramma* and insecticides. For instance, there is a premium price for organically produced crops that is often not applied to insecticide-treated produce. Using *Trichogramma* instead of insecticides preserves the endemic natural enemy complex and reduces the need for additional treatments to control secondary pests, and it reduces the risks to human and environmental health that are associated with insecticides (Pimentel et al. 1993, Smith 1996). If a strain of *Trichogramma* is discovered that can reduce *P. rapae* and *T. ni* populations below action thresholds, or if the cost for *Trichogramma* production can be decreased, then cabbage producers can recoup the cost of treatment, and the use of *Trichogramma* may be adopted. New devices for delivering *Trichogramma* to the field (Landis and Orr 1996, Hassan 1999), and the development of an in vitro rearing program for *Tri-*

chogramma (Nordlund et al. 1998) may result in reduced production costs.

Our research illustrates the competitive nature of *Bt* as a reliable and effective pest control agent for cruciferous Lepidoptera. The formulation of *Bt* used in this study is Lepidoptera-specific and has a short persistence in the field (Behle et al. 1997). These characteristics minimize nontarget impacts of pest control in the cropping systems where *Bt* is used and have allowed *Bt* to be effectively integrated with *Trichogramma* biological control programs in the past (Oatman et al. 1983, Losey et al. 1995). Further research into integrating releases of *Trichogramma* with current pest management practices in the cabbage system may lead to a long-term solution for control of cruciferous Lepidoptera.

Acknowledgments

We thank Amanda Jacobson, Sam Lockner, Katie Vogt, Tim Wheeler, and the staff of the Rosemount Experiment Station for their assistance in producing this research. Gary Pahl provided transplants in 2000. Beneficial Insectary provided *Trichogramma brassicae*. John Pinto authenticated *T. brassicae*. Abbott Laboratories and Dow AgroScience provided pesticides, and Loveland Industries provided the adjuvants used with the pesticides. Special thanks to Vince Fritz, William Hutchison, Dharma Sreenivasam, and Robert Wiedenmann for their comments on earlier versions of this manuscript. This research was funded by the North American Pesticide Impact and Assessment Program and the Minnesota Department of Agriculture's Biological Control Granting Program. This research has been supported in whole or in part by the University of Minnesota Agricultural Experiment Station.

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Received for publication 10 December 2001; accepted 29 June 2002.