

# Interactions Between Large-Scale Inundative Releases of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) and Naturally Occurring Spruce Budworm (Lepidoptera: Tortricidae) Parasitoids

R. S. BOURCHIER<sup>1</sup> AND S. M. SMITH<sup>2</sup>

Canadian Forest Service, Sault Ste Marie, P.O. Box 490, Sault Ste. Marie, ON, Canada P6A 5M7

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**ABSTRACT** A total of 480 million females of the egg parasitoid *Trichogramma minutum* Riley was aerially released on 30 ha of boreal forest infested by the spruce budworm, *Choristoneura fumiferana* (Clemens), in Ontario, Canada. *T. minutum* were released in parasitized eggs of the factitious host, the Mediterranean flour moth, *Ephestia kuehniella* Zeller. Emergence of released *T. minutum* peaked at 80%, 5 d after the parasitoid releases. *T. minutum* were active attacking sentinel egg masses in the release plots up to 15 d after the 1st parasitoid release. The mean rate of parasitism of budworm egg masses by *T. minutum* was 68% in 3 treatment plots versus <2% in the matching control plots. The reduction in budworm density in the treatment plots from egg parasitism by *T. minutum* was maintained in the overwintering 2nd-instar budworms (October 1993) and for the 6th-instar budworms sampled in June 1994. Additional foliage protected in the treatment plots was between 37 and 51%. The rate of parasitism by the early-instar parasitoid *Apanteles fumiferanae* Viereck declined after the reduction of budworm populations in the treatment plots. In contrast, parasitism by the late larval tachinid complex, consisting primarily of *Winthemia fumiferanae* Tothill and *Lypha setafacies* (West), increased in the treatment plots. Aerial inundative releases with *T. minutum* can provide effective short-term population suppression of spruce budworm and significant foliage protection. The releases also complement the late larval parasitoids that have been suggested to be important in initiating a budworm population collapse.

**KEY WORDS** *Trichogramma*, *Apanteles fumiferanae*, *Winthemia fumiferanae*, *Lypha setafacies*, egg parasitoids, biological control

THE SPRUCE BUDWORM, *Choristoneura fumiferana* (Clemens), is a serious defoliator of spruce-fir forests in North America. Its biology and population dynamics have been studied extensively (Morris 1963; Royama 1984, 1992) with the principal objective of understanding what causes populations to cycle, and from a forest-management view, what causes pest outbreaks. Numerous budworm population studies have noted an increase in the rate of late larval parasitism during the final years of population outbreaks (Dowden et al. 1948, Jaynes and Drooz 1952, McGugan and Blais 1959, Blais 1960, Miller 1963). Three of the important parasitoids in this complex are 2 Diptera (Tachinidae), *Winthemia fumiferanae* Tothill and *Lypha setafacies* (West) and a braconid wasp, *Meteorus trachynotus* (Viereck). Royama (1992) showed that there were 2 distinct components that govern the dynamics of a budworm population. The 1st component is a long-term oscillation in late larval survival (associated with parasitism) that results in the underlying population cycle of between 30 and 40 yr; the 2nd component is

rapid random fluctuations in the budworm recruitment rate expressed as the ratio of the number of eggs to the number of locally emerged moths (E/M ratio) that affects the yearly rate of change in population density. Budworm populations rise to an outbreak plateau, where they fluctuate because of perturbations resulting from changes in the budworm recruitment rate (E/M ratio). Outbreaks tend to persist because the natural enemy complex is usually ineffective because of the suppressive factors of their own natural enemies or a lack of alternative hosts (Royama 1992). Over the years of high budworm density, however, the power of this late larval complex can become sufficiently strong to bring the budworm population down (Royama 1992).

Currently the most commonly used control tactic for spruce budworm populations in Canada is aerial application of the microbial insecticide *Bacillus thuringiensis*. The primary objective when spraying *B. thuringiensis* is to protect between 50 and 60% of the current year foliage (Kettela 1995). Alternative control tactics include the use of *Trichogramma minutum* (Riley), an egg parasitoid of many forest Lepidoptera, including the spruce budworm. Natural rates of parasitism by *T. minutum* usually range between 5 and 15%. There are however historical reports of parasit-

<sup>1</sup> Corresponding Author, current address: Agriculture and Agrifood Canada, P.O. Box 3000, Lethbridge, AB, Canada T1J 4B1. e-mail: bourchierR@em.agr.ca

<sup>2</sup> Faculty of Forestry, University of Toronto, Toronto, ON, Canada M5S 3B3.

ism reaching as high as 77% (Miller 1963, Houseweart et al. 1982, Carrow 1990). In the early 1980s, a project was initiated with *T. minutum* to test whether the parasitoid could provide effective foliage protection when used in an inundative release. A double application of 12 million female parasitoids per hectare was shown to provide egg parasitism rates of up to 80% in 1-ha release plots, which resulted in reductions of 80% in the overwintering 2nd-instar larvae. These population reductions provided effective foliage protection (>50%) in the year after the parasitoid releases (Smith et al. 1990).

The 1980 releases were a combination of aerial and ground applications with release rates replicated over multiple years, depending on the availability of parasitoids. In 1993, we had sufficient numbers of parasitoids available for a larger scale field trial with replication. Our objectives in this study were to scale up aerial application methods for *Trichogramma* to test if the results from the 1980s were consistent in larger plot sizes, and to assess the interactions between imposed mortality caused by egg parasitoids and naturally occurring budworm parasitoids. The budworm parasitoids studied included 2 early-instar parasitoids, *Apanteles fumiferanae* Viereck and *Glypta fumiferanae* (Viereck) and the late larval tachinids *W. fumiferanae* and *L. setafacies*. The late larval tachinids were of primary interest because they form part of the complex that has been suggested to play a role in budworm population collapses (Royama 1992).

### Materials and Methods

**Study Site.** The study site was located near Black Sturgeon Lake, ON, Canada (48° 2' N, 88° 5' W), in plots similar to those described by Lethiecq and Régnière (1988). A spruce budworm outbreak has persisted in the area since 1981; the outbreak has been monitored in a permanent sample plot by the Canadian Forest Service. For our study, six 10-ha plots were selected in June of 1993; treatment and control plots were paired based on proximity, similarity of tree density and age, and tree species composition; 3 plots received *T. minutum* applications and 3 plots were used as controls.

**Trichogramma Release Methodology.** Parasitoid Colony. *T. minutum* used for the release were collected initially from spruce budworm egg masses in Quetico Provincial Park, ON, Canada (48° 7' N, 91° 1' W), during July 1988. This parasitoid line was maintained at the mass production facility (Ciba-Biologicals, Guelph, ON, Canada; now Beneficial Insectary) on the Mediterranean flour moth, *Ephesia kuehniella* Zeller, eggs for ≈130 generations before the parasitoid releases.

Parasitoids were released aurally using a Bell 47 helicopter equipped with a modified Brome seeder (Hope et al. 1990). The release rate was 16 million female parasitoids per hectare, in 2 applications of 8 million females per hectare, spaced 7 d apart. Release timing was based on the flight period of adult budworms as assessed using pheromone traps in the plots.

The 1st release date was set for 3 d after the 1st moths were trapped and the 2nd release was 7 d later (Smith et al. 1990).

**Trichogramma Emergence and Activity.** The timing and proportion of parasitoid emergence from the flour moth eggs, for all plots, was assessed using 10 subsamples of the release material placed in separate vials that were held at field conditions. Each day after the release, a vial was moved to the freezer. Plotting the number of parasitoids that had emerged at field conditions in each vial provided an estimate of cumulative parasitoid emergence.

Parasitoid activity in the field plots was monitored using sentinel egg masses consisting of a spruce budworm egg mass on balsam fir foliage (Smith et al. 1986; see Wallace and Smith [1995] for photographs). These sentinel egg masses were placed in the field 3 d before the 1st release date. Ten sentinel stations were placed along a central transect in each plot with at least 20 m between each sentinel station. A station consisted of a single rope pulley, similar to Wallace and Smith (1995); 1 sentinel egg mass was placed at the top of the pulley, ≈½ way up the bole of the tree and a 2nd sentinel egg mass was placed at 1.5 m above ground. Sentinel egg masses were changed every 3 d and exposed egg masses were placed in gel caps to assess parasitism (number of black spruce budworm eggs) and rate of emergence.

**Spruce Budworm and Parasitoid Population Densities.** Spruce budworm populations in treatment and control plots were sampled 5 times. Larval populations were sampled at the 3rd and 6th instars (June 1993) before the *Trichogramma* release. After the parasitoid release, budworm egg masses were sampled in August 1993, overwintering 2nd instar budworm (L2) were sampled in October 1993, and 6th instar budworm (L6) were sampled in June 1994. The sample unit was a 45-cm branch tip taken from the midcrown of codominant balsam fir (*Abies balsamea* L.). Budworm densities were expressed in terms of insects per kilogram of fresh foliage (Régnière et al. 1989). Trees were selected along a 20 by 150-m transect through the center of each plot. Overwintering budworm sampled in October 1993 were removed from the sample branches using the washing technique detailed in Dorais and Kettela (1982). Parasitism by overwintering parasitoids (October 1993 sample) was assessed by dissection (Brown 1946). Budworm larvae sampled in June 1994 were picked off the foliage and reared in vented-plastic containers with balsam-fir foliage to assess late larval parasitoid emergence.

Branch sampling in June 1993 provided density estimates for the budworm and for 2 early-instar budworm parasitoids, *A. fumiferanae* and *G. fumiferanae*, before our intervention with *T. minutum*. Branch sampling of budworm egg masses in August gave a direct measurement of the impact of the *T. minutum* release on the egg density of the budworm in the treatment and control plots. The October branch sample provided an estimate of both the densities of the overwintering budworm and the 2 early-instar parasitoids, *A. fumiferanae* and *G. fumiferanae*, after the *T. minu-*

*tum* treatment. The June 1994 sample tested if direct effects of reduced population densities observed on budworm egg masses in 1993 were maintained in the next generation, and if the rate of parasitism by late larval tachinid parasitoids of the spruce budworm differed in treatment and control plots.

Foliage protection was assessed after the completion of budworm feeding in July 1994. Samples were 45-cm branch tips taken from the midcrown of codominant balsam fir sampled along the central transects. Twenty-five shoots on 10 sample branches from each plot were scored on a 6-point qualitative scale (modified Fettes classes; Dorais and Kettela 1982); where 1 = no defoliation; 2 = 1–25% defoliation; 3 = 26–50% defoliation; 4 = 51–75% defoliation; 5 = 76–100% defoliation, and 6 = shoot needles and axil destroyed. Foliage protected was calculated using a weighted mean of the defoliation index in control plots and treatment plots: percentage of foliage protected =  $([\text{mean foliage index control} - \text{mean foliage index treatment}] / \text{mean foliage index control}) * 100$  (Dorais and Kettela 1982). The distribution of shoots across damage categories were pooled for the treatment and control plots and compared statistically using a  $2 \times 6$  contingency table (Wilkinson 1997).

**Statistical Analysis.** Mean population densities of budworm larvae per kilogram of foliage were calculated for treated and control plots. The effects of the *T. minutum* applications were expressed using Abbott's formula (Abbott 1925, Dorais and Kettela 1982). The comparison of population densities before and after the parasitoid release, in treatment and control plots that were paired before the experiment, provides a measure of the percentage of population reduction that can be attributed to the treatment. The population reductions (Abbott's values) for the 3 paired treatment and control plots were then tested against the null hypothesis that the effect attributable to treatment was zero using a 1-tailed *t*-test.

Larval parasitism by naturally occurring parasitoids was expressed as an odds ratio calculated by taking the log of the ratio between the number of sample budworm larvae parasitized and the number of budworm larvae not parasitized (Crawley 1993). Odds of parasitism by early or late instar parasitoids (dependent variable) were compared in treatment and control plots by using a logistic regression model. This model enables the use of binary response variables, such as the presence or absence of parasitism, linked to both continuous and categorical independent variables (Hosmer and Lemeshow 1989, Crawley 1993). The independent variables tested for the model included the pairing of treatment and control plots (blocking variable), and the presence or absence of *Trichogramma* releases in the plots.

## Results

**Trichogramma Emergence and Activity.** A total of 240 million *T. minutum* females was released on each of 2 dates (15 and 21 July 1993) in the three 10-ha release plots (160 million *T. minutum* females in total

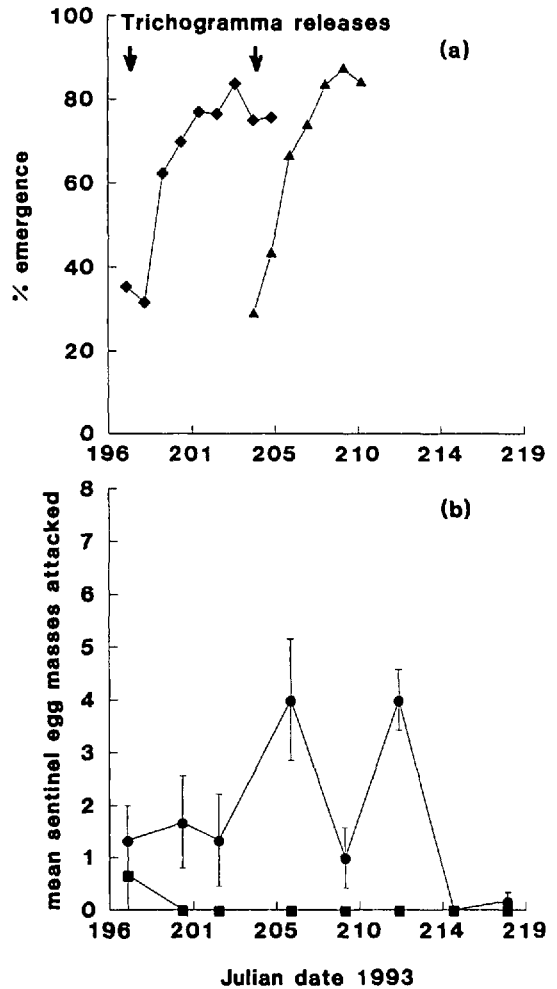


Fig. 1. (a) Emergence curves for *T. minutum* released on 15 July (JD 197,  $\blacklozenge$ , release 1, 1st vertical arrow) and 22 July (JD 204,  $\blacktriangle$ , release 2, 2nd vertical arrow) 1993 near Black Sturgeon Lake, ON, Canada. (b) Mean number of sentinel egg masses of the spruce budworm that were attacked in treatment ( $\bullet$ ) and control plots ( $\blacksquare$ ) after inundative release with *T. minutum* released on 15 July (JD 197) and 22 July (JD 204) 1993.

per plot). Percentage of emergence of parasitoids from Mediterranean flour moth eggs for both releases peaked 5 d after the release at  $\approx 80\%$  of the parasitized eggs (Fig. 1a). Parasitoids were active in the release plots until at least the 30 July 1993 (Julian date 212) based on parasitism of the sentinel egg masses (Fig. 1b). The lag before the 1st peak in Fig. 1b may be a function of the delayed emergence of the parasitoids. The long activity period suggests that parasitoids may have been finding food sources in the field to remain active; parasitoids that are unfed in the laboratory usually die within 2 d of emergence (Leatemia et al. 1995).

**Spruce Budworm Population Density.** From the August 1993 egg mass sample, the percent parasitism by *T. minutum* of field-collected budworm egg masses

Table 1. Percent parasitism by *Trichogramma minutum* of spruce budworm egg masses in August 1993 and mean population densities of the spruce budworm, before and after the parasitoid releases in July 1993

	Budworm Egg Masses August 1993		Mean $\pm$ sem. SBW Density (budworm/kg foliage)		
	Total percent parasitism by <i>Trichogramma</i>	Total number of egg masses sampled	June 1993 <sup>1</sup>	October 1993 <sup>2</sup>	June 1994 <sup>3</sup>
Treated plots	68.6%	321	194.3 $\pm$ 45.6	33.7 $\pm$ 7.6	45.3 $\pm$ 33.9
Control plots	1.6%	181	195.7 $\pm$ 23.4	117.0 $\pm$ 53.6	114.0 $\pm$ 56.4
Mean % Reduction due to treatment <sup>4</sup>				58.3 $\pm$ 11.4% p = 0.036	65.4 $\pm$ 9.6% p = 0.021

<sup>1</sup> Density estimate prior to *T. minutum* applications on 15 July and 22 July 1993; larvae were picked from foliage.

<sup>2</sup> Density estimate of overwintering 2nd instar budworm; used washing technique to remove larvae from foliage (Dorais and Kettela 1982).

<sup>3</sup> Density estimate of 6th instar budworm; larvae were picked from foliage.

<sup>4</sup> Mean of population reduction due to treatment using Abbott's formula (Abbott 1925),  $n = 3$  paired treatment and control plots.  $P$  value is for one-tailed  $t$ -test of the null hypothesis that the reduction due to treatment was zero.

in the 3 treatment plots was 64.8, 79.1, and 62.1%, with samples of 108, 110, and 103 egg masses, respectively. Control plots that were paired with treatment plots before the release had 3.6, 0, and 1.3% parasitism by *T. minutum*, respectively, from samples of 56, 51, and 74 budworm egg masses. Egg mass samples in the treatment and control plots were taken from the same number of branch samples. Percentage of parasitism across all egg masses was 68.6% in the treatment plots versus 1.6% in the control plots (Table 1).

The differences in the population density of spruce budworm in control and treated plots at the August 1993 egg mass sample were maintained in both the overwintering budworm sample in October 1993 and in the late larval budworm sample in June 1994 (Table 1). Budworm densities per kilogram of foliage in treatment plots were less than half of densities in the control plots after the *Trichogramma* application (Table 1). The mean percentage of reduction in budworm population density caused by treatments from the 3 treatment plots paired with their respective control plots was 58.3% in October and 65.4% in June 1994 (Table 1; Abbott's formula; Abbott 1925, Dorais and Kettela 1982). The percent reductions caused by treatment for both dates were significantly different from 0 (Table 1,  $P = 0.036$  and  $P = 0.021$ , respectively).

The *Trichogramma* release provided significant foliage protection; (comparison of damage categories in the treatment and control plots:  $\chi^2 = 383.2$ ;  $P < 0.001$ ). In the treatment plots, 68.5% of the shoots had no damage and 7.4% of the shoots had >75% damage (category 5 + category 6; Fig. 2a); whereas in the control plots, 22.2% of the shoots were undamaged and 44.8% of the shoots had >75% damage (category 5 + category 6; Fig. 2b). Additional foliage protected by the parasitoid treatment, calculated using the formula in the methods section, was between 37 and 51% in treated plots. The lower number resulted when branches from all control plots were included in the calculation, whereas 51% resulted when control plot 1 was excluded. In July 1994, many of the trees in control plot 1 were dead or had no visible new foliage; branch samples were taken from those trees that could be found with visible foliage and thus we suspect we may have underestimated the amount of foliage damage in the entire plot.

**Parasitoid Population Densities.** Parasitism by the early-instar parasitoids after the reduction in budworm densities resulting from the *T. minutum* releases was assessed in October 1993. There was a significant reduction in the odds of parasitism by *A. fumiferanae* in all treatment plots when compared with their respective control plots (Fig. 3a); the simplest best fit logistic model ( $G = 30.3$ ,  $df = 3$ ,  $P < 0.001$ ; residual deviance = 2.32,  $df = 2$ ) included the blocking factor (pairing of plots;  $P = < 0.001$ ) and the *T. minutum* application (treated/control;  $P = 0.04$ ) as significant factors. Fitting a similar model to the odds of parasitism by *A. fumiferanae* before the *T. minutum* application there was no significant difference between treated and control plots ( $G = 1.02$ ,  $df = 3$ ,  $P = 0.80$ ; residual deviance = 3.91,  $df = 2$ ), confirming the

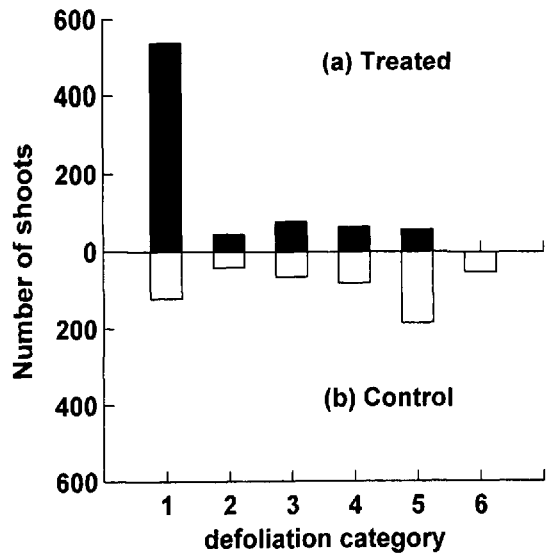


Fig. 2. Number of shoots in 6 damage categories where 1 = no defoliation; 2 = 1-25% defoliation; 3 = 26-50% defoliation; 4 = 51-75% defoliation; 5 = 76-100% defoliation and 6 = shoot needles and axil destroyed in (a) 3 *Trichogramma* release plots (number of shoots = 782) and (b) 2 control plots (number of shoots = 543) located near Black Sturgeon Lake, July 1994. Comparison damage categories in the treatment and control plots was statistically significant ( $\chi^2 = 383.2$ ;  $P < 0.001$ ).

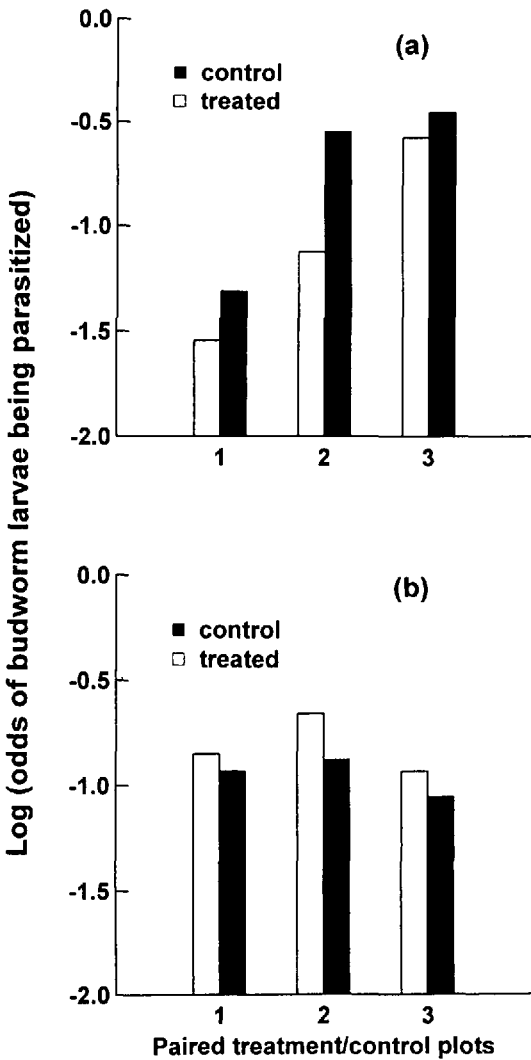


Fig. 3. Log (odds of parasitism) in paired treatment and control plots: (a) for *A. fumiferanae* attacking overwintering spruce budworm larvae sampled in October 1993; treatment  $-1.08 \pm 0.28$ ; (mean  $\pm$  SE); control  $-0.77 \pm 0.27$ ; (b) for the tachinid complex attacking the late-larval stages of budworm in June 1994; treatment  $-0.81 \pm 0.08$ ; control  $-0.96 \pm 0.05$ .

impact of the *T. minutum* release on the early-larval parasitoid. We were unable to draw conclusions about the impact of the *T. minutum* release on *G. fumiferanae* because the rate of parasitism by this parasitoid was very low (<1%) in all plots both before and after the *T. minutum* release.

Based on the June 1994 sample, there was a significant increase in the late larval tachinid complex, primarily *W. fumiferanae* and *L. setafacies*, following the reduction in budworm densities resulting from the *T. minutum* releases. There was a significant increase in the odds of parasitism by tachinids in all treatment plots when compared with their respective control plots (Fig. 3b); the simplest best fit logistic model, ( $G = 12.04$ ,  $df = 3$ ,  $P < 0.001$ ; residual deviance = 0.6,

$df = 2$ ) included the blocking factor (pairing of plots;  $P = 0.03$ ) and the *T. minutum* application (treated/control;  $P = 0.02$ ) as significant factors.

Discussion

To date, the 1993 *T. minutum* releases at Black Sturgeon Lake are the largest inundative program involving aerial application of parasitoids in North American forests. Our results confirm the work of Smith et al. (1990) conducted in smaller plots (1 ha) that inundative releases of egg parasitoids can cause significant population reductions of the spruce budworm and can provide effective foliage protection (Table 1; Fig. 2). The redistribution of budworm populations that is known to occur as adult moths (Greenbank 1963, Greenbank et al. 1980), and as early-instar larvae (Miller 1958), did not cause a population increase in the treatment plots after the *Trichogramma* application in 1993. If there was an in-flight of moths into the treatment plots, after the 1993 *Trichogramma* application, it was insufficient to remove the treatment effects of the *T. minutum* releases. Egg parasitoids were likely present to attack any new egg masses that were laid by immigrants up until the end of July.

The 1994 densities of both *A. fumiferanae* and the late larval tachinid complex would have been set by the budworm density in 1993 before our intervention with *T. minutum*. This initial 1993 parasitoid density may have been subsequently modified by abiotic factors or the availability of alternate hosts; however, these factors would likely have had a similar impact in both treated and control plots. After our intervention with *T. minutum*, there should have been a lot of larval parasitoids chasing after significantly fewer hosts in the treatment plots. The larval parasitoids could have responded by increasing their rate of apparent parasitism (Miller 1963) or they could have dispersed. Our results suggest that parasitoid guilds responded differently. The late larval tachinid complex increased their rate of apparent parasitism whereas the rate of parasitism by *A. fumiferanae* declined in release plots.

*Apanteles fumiferanae* has been frequently studied because it is found in most budworm populations (Brown 1946, Miller 1963, Nealis 1988). Its impact however rarely goes >30%; and the parasitoid is not able to multiply fast enough to control the budworm, possibly because of the actions of a complex of hyperparasitoids (Royama 1992). In contrast, an increase in the rate of parasitism by the late larval tachinid parasitoids *W. fumiferanae* and *L. setafacies* may assist in creating the conditions where a budworm population collapse can occur; it may help make the power of the late larval complex sufficiently strong to bring the budworm population down (Royama 1992). We were not able to assess if the observed changes in late larval parasitism had an effect on budworm populations. This possibility would have to be assessed in a longer-term population study of budworm dynamics after perturbations.

The implications of this study for budworm management are associated primarily with the stage of an

outbreak that is being targeted. Integrating a population control program with late larval parasitoids will only work to create the conditions associated with a local budworm population collapse, provided that the late larval parasitoids are already present in the population and that the control tactic does not significantly reduce their numbers (Waage et al. 1985). Parasitoid complexes change dramatically between the endemic (Miller and Renault 1976) and the epidemic (Miller 1963, Royama 1992) stages of the budworm population. *L. setafacies* and *W. fumiferanae* are not common in endemic budworm populations or in the very early stages of a budworm outbreak. An increase in apparent parasitism by these parasitoids may not be observed in association with a control tactic if it is too early in development of a budworm outbreak for the parasitoids to be present.

The principal control tactic available for budworm control, the aerial application of either *B. thuringiensis* or chemical insecticides, may inhibit the increase in apparent parasitism by late larval parasitoids because the tactic may have a direct effect on survivorship of parasitized budworm larvae. Shifting the timing of *B. thuringiensis* sprays toward later larval stages resulted in increased survival of the early-instar parasitoid *A. fumiferanae* in comparison to early-spray plots (Nealis et al. 1992). There was still significant *A. fumiferanae* mortality however in the late-spray plots because the sprays killed some parasitized hosts. Delaying *B. thuringiensis* applications to conserve early-instar parasitoids may remove significant numbers of budworm larvae that were parasitized by late larval parasitoids and might prevent their numbers from rising to levels associated with late-stage budworm outbreaks; this interaction requires further investigation. Application of *T. minutum* at the egg stage avoids any direct conflicts with late larval tachinids. There may be a conflict between *M. trachynotus* and the inundative release of *T. minutum* because the eggs of *Choristoneura rosaceana* (Harris), the overwintering host of *M. trachynotus* (Maltais et al. 1989), are likely present at the time of *T. minutum* releases and may be susceptible to attack. Reduction in alternative hosts has been suggested to be a limiting factor for *M. trachynotus* attacking the spruce budworm (McCugan and Blais 1959).

Release rates for *T. minutum* in 1993 were  $\frac{2}{3}$  the levels used in the early 1980s and yet still provided a significant reduction in the budworm populations (Table 1) and significant foliage protection (Fig. 2). Compared with *B. thuringiensis*, however, the cost of using *T. minutum* is currently too high to be feasible as a pest control tool in forestry. Similar concerns were expressed about the cost of *B. thuringiensis* when it was compared with the available chemical insecticides early in its development process (van Frankenhuyzen 1993). In the future, the cost of using *Trichogramma* will be reduced by improvements in strain selection, rearing methodologies, and application techniques, areas that are all subjects of current research (Wajnberg 1995, Smith 1996).

The success of past biological control programs has often been a combination of luck and scientific understanding. *Trichogramma* spp. are some of the more studied parasitoids in the world because of their potential application in augmentative biological control (Wajnberg and Hassan 1994, Wajnberg 1995). The type of data collected for many of these studies is at the stage of demonstrating field efficacy: how many parasitoids are required to suppress host populations. Our study demonstrates the potential of linking biological control to the population dynamics of the target host. Parasitoids are used to inflict mortality at a critical stage in the target pest life cycle. The level of host mortality required from the biocontrol agent may be relatively low if the released natural enemy complements other stage-specific mortality factors. For our releases of the egg parasitoid *T. minutum*, we targeted the life-stage of the budworm associated with the 2nd component governing the dynamics of budworm populations, the E/M ratio (Royama 1992). *T. minutum* acts to reduce the E/M ratio by killing host eggs, which can in turn affect the level of late larval parasitism; the factor that has been linked to the long-term population cycle of the budworm (Royama 1992). It is conceivable that most inundative biological-control programs can be improved by linking the selection of the natural enemies to a vulnerable host stage based on host population dynamics and by using the inundative agent to complement naturally occurring mortality factors.

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