GROUND RELEASES OF *TRICHOGRAMMA MINUTUM* RILEY (HYMENOPTERA: TRICHOGRAMMATIDAE) AGAINST THE SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE)

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Can. Ent. 119: 251–263 (1987)

Abstract

During 1982 and 1984, ground releases of *Trichogramma minutum* Riley were assessed for control of the spruce budworm, *Choristoneura fumiferana* (Clemens), on 12- to 20-year-old, white spruce stands in northern Ontario. Maximum parasitism of susceptible egg masses was 16 and 87% following the release of 480 000 and 12 million female *T. minutum* per hectare, respectively. Releases at intervals of 1 week maintained parasitism of susceptible egg masses at constant levels throughout the oviposition period of spruce budworm. When parasitism of susceptible egg masses was maintained above 78.2% during the ovipositional period, total egg mass parasitism averaged 58.0% and resulted in an 80.3% reduction of overwintering 2nd-instar larvae. The optimal strategy for reducing spruce budworm was two releases of *T. minutum* at an interval of 1 week in the ovipositional period. This allowed a second generation of parasitoids to emerge from the spruce budworm eggs that were more efficient in maintaining high levels of parasitism than those emerging from the standard rearing host. Natural parasitism of spruce budworm egg masses was less than 4% and there was no carryover of parasitism in the years following inundative release. The rate of *T. minutum* release necessary to achieve effective mortality of spruce budworm during outbreak populations is discussed briefly.

Résumé

De 1982 à 1984, dans le nord de l'Ontario, des lâchers de *Trichogramma minutum* Riley contre la tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clem.), ont été évalués dans des peuplements d'épinette blanche âgés de 12 à 20 ans. Le taux naturel de parasitisme des masses d'oeufs de tordeuse était moins de 4% et aucune présence de parasitisme était detectée dans les années suivant les lâchers. Les taux maximaux de parasitisme étaient de 16 et 87% suivant des lâchers de 480 000 et 12 millions de femelles *T. minutum* par hectare respectivement. Les lâchers à intervale de 1 semaine pendant la période de ponte d'oeufs de la tordeuse maintenaient des taux de parasitisme constants. Quand le taux de parasitisme était maintenu au-delà de 78% pendant la période de ponte d'oeufs, le taux entier de parasitisme était 58% et entraînait une réduction de 80,3% des deuxièmes stades larvaires. La stratégie optimale pour l'emploi des lâchers de *T. minutum* contre la tordeuse était deux lâchers à intervale de 1 semaine tôt pendant la période de ponte d'oeufs. Ceci permettait une deuxième génération de parasitoïde d'éclore sur le terrain et ceux-ci étaient plus efficaces que ceux provenant de l'hôte de remplacement. Le taux de lâcher de *T. minutum* requis pour réduire les populations épidémiques de tordeuse est discuté brièvement.

Introduction

To protect Canada's boreal forest from the current outbreak of spruce budworm, *Choristoneura fumiferana* (Clemens), aerial spraying programs, using insecticides, are commonly employed. Growing public concern and opposition to the use of insecticides on public-owned forests can disrupt forest protection programs. To maintain effective forest management in the future, therefore, alternate, more acceptable methods of spruce budworm control must be provided.

Egg parasitoids in the genus *Trichogramma* have been used successfully as biological control agents in several countries. Although the impact of these egg parasitoids on pest populations of agricultural crops is well documented (Parker *et al.* 1971; Oatman and

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Platner 1971, 1978; Stinner 1977; Ridgway *et al.* 1981; Hassan 1982), little information is available on their potential for controlling forest insects (Kang-Jou 1980/1981; Walter 1983; Houseweart *et al.* 1984*a*). *Trichogramma minutum* Riley is the principal egg parasitoid of spruce budworm in eastern North America. Its impact upon spruce budworm populations is considered low (Morris 1963) because natural levels of parasitism are highly variable, and this species relies on alternate hosts to maintain its population throughout the year (Jennings and Houseweart 1983; Houseweart *et al.* 1984*b*).

Inundative releases of *T. minutum* eliminate the need for alternate hosts and provide a large number of parasitoids during the period of spruce budworm oviposition. Houseweart *et al.* (1984*a*) showed that parasitism of spruce budworm eggs following three closely timed aerial releases of *T. minutum* was increased by 3% and concluded that this parasitoid could have a significant impact upon spruce budworm populations. They suggested that multiple releases of *T. minutum*, broadcast or uniformly spread over forest stands, for control of the spruce budworm warranted further investigation, particularly in environmentally sensitive areas. During 1982 and 1984, we assessed the potential of using broadcast, inundative releases of *T. minutum* from points on the ground to suppress outbreak populations of spruce budworm in northern Ontario. Our objectives were to determine the effect of different timings, frequencies, and rates of release on egg parasitism as well as their subsequent impact upon larval populations. Although not strictly the goal of inundative release, we also examined the ability of *T. minutum* to carry over or survive in those years following inundative release (i.e. maintain higher parasitism than in control areas).

Materials and Methods

The experimental plots were located near Hearst, Ontario (50°N, 84°W) in 12- to 20-year-old, white spruce plantations. The stands comprised 37% balsam fir, *Abies balsamea* (L.), 24% white spruce, *Picea glauca* (Moench) Voss, 28% poplar, *Populus* species, and, from 1980 to 1984, were subjected to outbreak populations of spruce budworm (i.e. greater than 30 egg masses per square metre foliage). In 1982, seven sample plots, each 50 by 50 m (0.25 ha), were established in these stands with a minimum distance of 600 m separating each plot. Plots 2, 4, and 6 did not receive releases in 1982 and were used as controls (Table 1). Because of the low level of natural parasitism observed on these control plots during 1982, only plot 2 remained as a control in 1983. A meteorological station 15 km from the study plots recorded daily weather conditions.

Trichogramma minutum released in this study were originally from 10 parasitized spruce budworm egg masses collected in Plummer Twp., Ontario (46°N, 84°W) during the summer of 1981. This stock of parasitoids was not rejuvenated by new collections from the field. The parasitoids were maintained during 1981 and 1982 on the Mediterranean flour moth, *Anagasta kuehniella* (Zeller), at the Biological Control Laboratory, University of Guelph. In 1983, eggs of the Angoumois grain moth, *Sitotroga cerealella* (Olivier), were substituted as hosts. Rearing on this host was done principally (90%) at Rincon Vitova, Oak View, California, USA, and the remainder were reared at the Biological Control Laboratory in Guelph, Ontario.

Release of parasitoids. Several different strategies for ground release were tested by varying the timing and frequency of application. In 1982, single releases were made early (8 July) in plot 1 or late (14 July) in plot 5 during spruce budworm oviposition. Plots 3 and 7 received releases on both dates (double release). In 1983, three releases were conducted with material from each rearing source being combined. Five different release strategies were used, one on each plot: (1) single early (7 July) release in plot 4; (2) single late (21 July) release in plot 6; (3) double early (7 and 14 July) release in plot 1; (4) double late (14 and 21 July) release in plot 5; and (5) triple (7, 14, and 21 July) release in plot 3. The numbers of female *T. minutum* released on each plot are given in Table 1.

Table 1. Allocation of *Trichogramma minutum* to field study plots near Hearst, Ontario, during 1982 and 1984

Sample plot (0.25 ha)	Year	Release strategy	Release date	No. *T. minutum* released (10^6 ♀/ha)
1	1982	Single early	8 July	0.24
	1983	Double early	7, 14 July	10.8, 12.4
2	1982	Control	—	—
	1983	Control	—	—
3	1982	Double	8, 14 July	0.24, 0.24
	1983	Triple	7, 14, 21 July	10.8, 12.4, 12.8
	1984	Control	—	—
4	1982	Control	—	—
	1983	Single early	7 July	10.8
5	1982	Single late	14 July	0.24
	1983	Double late	14, 21 July	12.4, 12.8
6	1982	Control	—	—
	1983	Single late	21 July	12.8
7	1982	Double	8, 14 July	0.24, 0.24
	1983	Control	—	—
	1984	Control	—	—

The parasitoids were shipped to the field in eggs of the rearing hosts, *A. kuehniella* and *S. cerealella*, with over 80% programmed by the temperature of rearing to emerge in 24 h. The eggs were attached with distilled water to sheets of cardboard and transported under cool (less than 17°C), dark conditions. A subsample (ca. 1000 host eggs) was taken from each rearing source to determine the sex ratio, longevity, and fecundity of the parasitoids. The expected number of female parasitoids provided by the rearing source was used to divide the sheets of cardboard evenly into smaller cards. These cards were then placed in paper cups for protection and taken to the field. To achieve a uniform distribution, the cups were attached to release stakes in the field, 25 cm high, in a 7 by 7 m grid within each plot (Smith *et al.* 1986). Three weeks after each release, 10 cards (ca. 10 000 host eggs per card) were selected randomly from each release plot and successful parasitoid emergence calculated. These estimates combined with the sex ratio taken from the previous subsample provided information on the actual number of female *T. minutum* released per hectare.

Parasitism of sentinel egg masses. Sentinel egg masses were used to determine natural levels of parasitism as well as the extent and duration of parasitoid activity following release. Sentinel egg masses consisted of fresh egg masses laid on twigs of balsam fir by spruce budworm fed in the laboratory on both artificial diet and natural foliage. Three sentinel egg masses were placed in the upper, middle, and lower crown of each sample tree by means of a pulley system (Smith 1984; Wallace, person. comm.). The sample trees consisted of 17 balsam fir or white spruce per plot located in random clumps of three or four trees, each near the center of a plot. The distance of each sample tree from the nearest release stake ranged from 0 to 4.2 m but did not affect parasitism of sentinel egg masses (i.e. parasitism was not measurably higher on trees closer to the release points). Sample trees were 5.4 (SE = ± 0.2) m in height with a diameter breast height of 6.8 (± 0.3) cm and each exhibited from 10 to 50% spruce budworm defoliation. Because spruce budworm eggs are only acceptable for parasitism by *T. minutum* at a relatively young physiological age, before the head capsule of the embryo appears (Houseweart *et al.* 1982), the sentinel egg masses were changed every 3 days from mid-June until the end of August in 1982 and 1983. This ensured a continuous supply of fresh, susceptible spruce budworm egg masses for parasitism in the field.

To determine rates of parasitism, all sentinel egg masses were held at field temperature in individual gelatin capsules (size 00). For those egg masses parasitized, records were kept on the date of emergence, the number of egg masses and eggs per egg mass parasitized, missing, or not hatched, and the sex ratio of emergents. The number of egg masses parasitized out of the total number of viable egg masses returning from the field constituted a measure of percentage egg mass parasitism. Percentage egg parasitism was calculated by multiplying the proportion of egg masses parasitized by the proportion of eggs parasitized within each egg mass. Rates of daily parasitism were then derived by dividing these percentages with the number of days the sentinel egg masses remained in the field (i.e. 3).

Parasitism of egg masses laid naturally. In 1983, total parasitism of spruce budworm egg masses laid naturally was determined at the end of the ovipositional period on that plot (plot 3) which received a triple release in 1983. Twenty-five branches, each of balsam fir and white spruce, were cut during mid-August from the upper-mid crown of randomly selected trees in both this plot and a control area, 15 km from the release site (Sanders 1980). Each branch was examined for egg masses laid by spruce budworm in the current year. The branches were searched until the first five egg masses from each had been recovered as per the procedure for surveying populations of spruce budworm by the Forest Insect and Disease Survey (FIDS). The egg masses were classified as parasitized if at least one egg per egg mass had turned black.

To compare the effect of different release strategies on parasitism of naturally laid budworm egg masses, a model that estimated daily spruce budworm oviposition was used in 1983 (Régnière 1983). The model required monitoring daily activity of male moths with sticky pheromone traps (Sanders 1981) and daily, on-site maximum/minimum temperatures during April, May, June, and July. The estimates generated by the model, combined with the daily rate of parasitism observed on the sentinel egg masses, were used to predict the total percentage of natural spruce budworm egg masses parasitized on each release plot in 1983. This calculation assumed (Smith 1984) that (1) at field temperatures during 1983, egg masses were susceptible to parasitism by *T. minutum* for 3 days (Houseweart *et al.* 1982; Lawrence *et al.* 1985) and (2) at a release rate of 12 million female *T. minutum* per hectare, a maximum of 87% of the susceptible egg masses on these stands could be parasitized (Smith 1984). Predicted parasitism was then compared with actual parasitism observed for egg masses laid naturally on branch samples from the triple release plot in 1983.

Impact upon larval populations. To assess the impact of egg mass parasitism on larval populations of spruce budworm, branch samples were collected in January of 1984. A total of 51 whole branches per plot, one each from the upper, middle, and lower crown of the 17 sample trees of balsam fir and white spruce were taken from both a control plot and the 1983 triple release plot 3. Overwintering 2nd-instar larvae were removed from the branches by soaking each branch in hot potassium hydroxide (5%) and filtering with hexane (Sanders 1980).

Potential for carryover. The survival of *T. minutum* following inundative release was evaluated by examining the level of parasitism carried over from year to year. Those plots receiving the highest applications of *T. minutum* in previous years were used to assess carryover (i.e. plot 7 in 1983 and plots 3 and 7 in 1984). Sentinel egg masses were placed on these plots in both years, throughout the period of spruce budworm oviposition.

Results and Discussion

Natural parasitism. Prior to our study, surveys in this area by the FIDS reported annual parasitism of spruce budworm egg masses by *T. minutum* to be consistently less than 5%. In 1982, before our first release, parasitism of sentinel egg masses was less than 4% and on the three control plots remained below 3% throughout the summer (Fig. 1). Similarly, in 1983, less than 1% of the sentinel egg masses were parasitized (Fig. 2). The increase in parasitism to 3% observed in 1982, prior to the releases, could represent a natural cohort or generation of *T. minutum* surviving through the winter of 1981/1982. Based on their generation time under field conditions, adult progeny of these parasitoids would be coincident with those being released. It is unlikely, however, that naturally occurring parasitoids would contribute significantly to elevated levels of parasitism on the release plots because we saw no numerical response in populations of *T. minutum* on the control plots following the peak in spruce budworm oviposition (2 July to 2 August) (Fig. 2*a*). This low activity by native *T. minutum* provided a reliable baseline for examining the effect of the inundative releases.

Timing of release. Weather conditions in the 3 weeks following release during 1983 were warmer, drier, and had more sunshine hours than the 2 weeks following release during 1982 (i.e. 21.9°C, 33.0 mm, and 11.1 h for 1983 vs. 15.9°C, 102.2 mm, and 5.4 h for 1982). The effect of this inclement weather on the success of ground releases using *T. minutum* has been discussed previously (Smith *et al*. 1986).

In 1982, following the early release (8 July), the cool, wet weather delayed both spruce budworm oviposition and *Trichogramma* emergence. Consequently, increased egg parasitism was not observed until the second release and the effect of timing could not be truly ascertained (Fig. 1*b* and Smith *et al*. 1986). Information on the impact of the different release strategies was obtained in 1983, using temporal information from the peaks in parasitism in the sentinel egg masses (Fig. 2*b*, 2*c*). In each of these curves, the second peak, approximately 12 days after an individual release, provided information on the relative availability of spruce budworm eggs because those parasitoids active in the field during the second peak were the progeny of parasitoids that had been released. The height of the second peak indicates the degree of successful parasitism and, therefore, the synchrony of the releases with spruce budworm oviposition.

Maximum parasitism by the second generation of *T. minutum* in 1983 was 92.2% following a single release on 7 July and 21.3% following a single release on 21 July (Fig. 2*c*). Considerably more spruce budworm eggs, therefore, were parasitized following the single early release than the single late release, suggesting a greater availability of eggs following the early release. Although a single middle release on 14 July was not conducted, the number of spruce budworm eggs available at this time was estimated from the two curves in Figure 2*b* between 24 July and 3 August, ca. 12 days following the second release. Maximum parasitism, in this case, averaged 54.5%, indicating that the two earlier releases were well synchronized with the natural ovipositional curve of the spruce budworm and had a greater impact upon spruce budworm populations than the last release.

Frequency of release. Multiple releases of *T. minutum* did not increase maximum observed parasitism but sustained it for a period of 1 week following each release. When *T. minutum* was applied at three 1-week intervals in 1983, parasitism of sentinel egg masses was maintained above 78.2% from 8 July until early August (Fig. 2*a*). Parasitism after the last release on 21 July was maintained by the second generation of parasitoids emerging from spruce budworm eggs laid naturally during the earlier releases. The longevity and fecundity of these parasitoids retained without food in the laboratory averaged 2.0 (± 0.3) days and 39.9 (± 5.8) eggs per female, respectively. In the field then, an energy source must have been obtained because parasitism was evident for 9 or 10 days following each release.

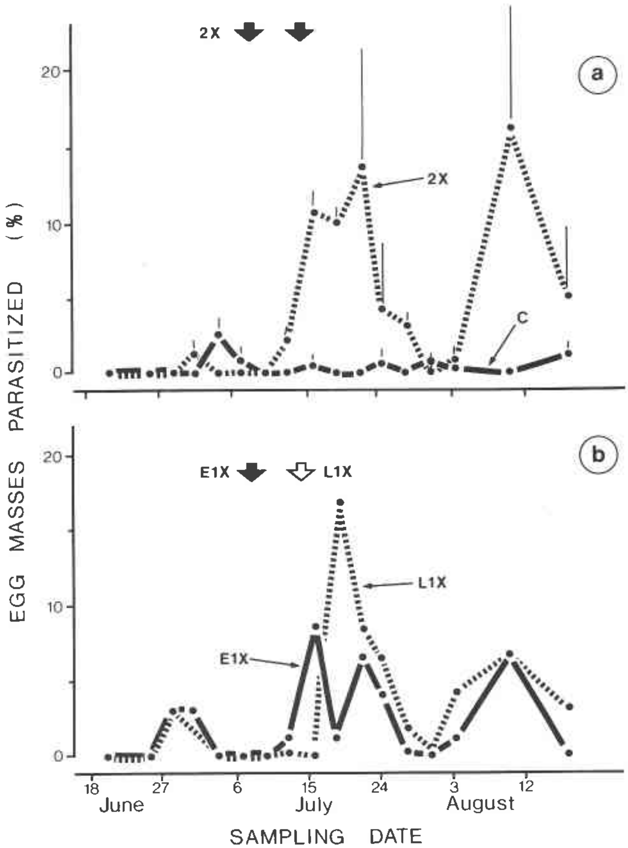

FIG. 1. Parasitism of susceptible spruce budworm egg masses following ground release of ca. 240 000 *Trichogramma minutum* females per hectare per release near Hearst, Ontario, in 1982. Arrows indicate release dates. (*a*) Solid line, three control plots, C; dotted line, two double release plots, 2X (8 and 14 July). Standard errors are shown as lines above each mean but represent equal variation below. (*b*) Solid line, one early single release plot, E1X (8 July); dotted line, one late single release plot, L1X (14 July).

Under forest conditions, sources of carbohydrate for hymenopterous parasitoids are found in aphid honeydew, dew, nectar, and/or pollen (Leius 1960).

To determine the best strategy for using *T. minutum* to suppress populations of spruce budworm, the impact of the different frequencies of release on total parasitism was examined. Given comparable numbers and quality of parasitoids released, total parasitism will depend upon the proportion of fresh, susceptible host eggs present in the field at any given time. The total parasitism of naturally laid egg masses for only one release strategy in 1983 was determined directly by sampling; on the triple release plot, where parasitism of sentinel egg masses was maintained above 78.2% throughout the period of spruce budworm oviposition, 58.0% of the egg masses laid naturally were parasitized.

For the remaining releases, total parasitism was estimated using information from the oviposition model (Régnière 1983). In 1983, adult moths were present in the field from 2 July to 2 August with peak flight around mid-July. As predicted by the oviposition model, the majority of spruce budworm egg masses was deposited between 10 and 23 July (Fig. 3). Using this prediction, the estimated total parasitism of egg masses laid naturally on the triple release plot was 59.0% (Table 2). This value compares favorably with that actually obtained by sampling (58.0%) and suggests that this approach can be used to examine

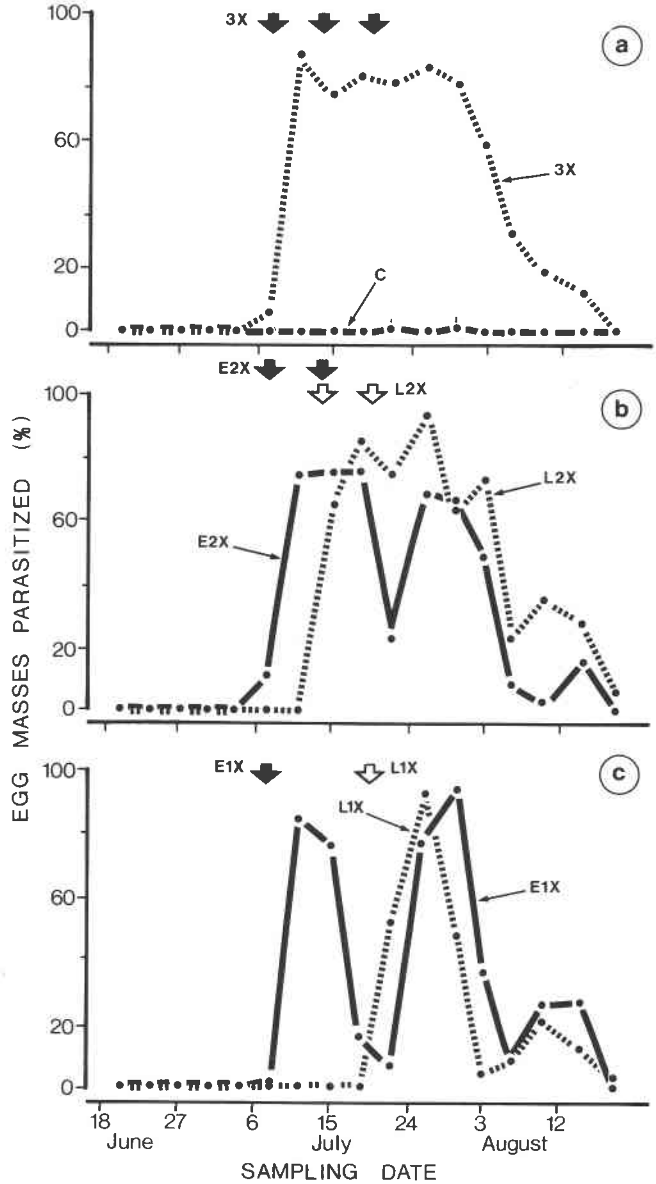

FIG. 2. Parasitism of sentinel spruce budworm egg masses following ground release of ca. 12 million *Trichogramma minutum* females per hectare per release near Hearst, Ontario, in 1983. Arrows indicate release dates. (*a*) Solid line, two control plots, C; dotted line, one triple release plot, 3X (7, 14, and 21 July). Standard errors are shown as lines above each mean but represent equal variation below. (*b*) Solid line, one early double release plot, E2X (7 and 14 July); dotted line, one late double release plot, L2X (14 and 21 July). (*c*) Solid line, one early single release plot, E1X (7 July); dotted line, one late single release plot, L1X (21 July).

total parasitism on those plots receiving releases at other frequencies. For the remaining strategies in 1983, therefore, the estimated, total parasitism was 16.9% (single early), 19.5% (single late), 43.7% (double early), and 60.1% (double late) (Table 2). Lawrence *et al.* (1985), using information from developmental studies, predicted that two releases early in the ovipositional curve would provide enough time for a second generation of *T.*

Table 2. Daily parasitism of sentinel spruce budworm egg masses and eggs following ground release of *Trichogramma minutum* during 1982 and 1983 near Hearst, Ontario

Year	Release strategy	Application rate (10^6 ♀/ha)	Parasitism of sentinel egg masses (%)			Parasitism of sentinel eggs (%)		
			Total*	Maximum†	Daily	Total*	Maximum†	Daily
1982	Single early	0.24	—	10.3	1.7	—	2.7	0.5
	Single late	0.24	—	18.9	2.8	—	6.1	1.0
	Double	0.48	—	15.5 (±5.6)‡	2.3 (±0.7)‡	—	6.2 (±2.4)‡	1.0 (±0.3)‡
	Mean	0.36	—	15.9 (±2.8)	2.3 (±0.3)	—	4.9 (±1.4)	0.8 (±0.2)
1983	Single early	10.8	16.9	82.2	17.4	7.2	58.6	10.7
	Single late	12.8	19.5	91.1	19.2	11.8	82.2	15.0
	Double early	10.8, 12.4	43.7	78.7	19.4	25.4	53.0	12.5
	Double late	12.4, 12.8	60.1	96.8	28.1	37.0	81.8	21.9
	Triple	10.8, 12.4, 12.8	59.0 (58.0)§	88.0	21.2	34.9	62.7	16.2
	Mean	12.0	—	87.4 (±3.2)	21.2 (±1.9)	—	67.7 (±6.1)	15.3 (±1.9)

*Estimated from model and parasitism of sentinel eggs.
†Highest value reached within 1 week of release.
‡Replicated on two plots, standard errors in parentheses.
§Actual value obtained from sampling the plot after oviposition.

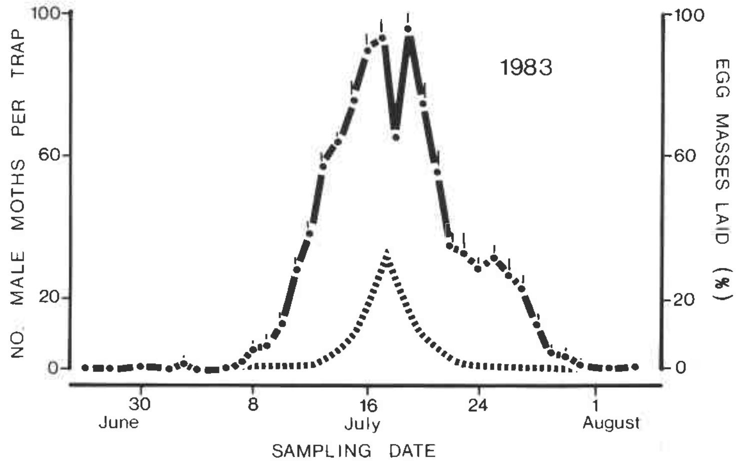

FIG. 3. Number of male moths collected daily in pheromone traps and the predicted ovipositional curve for spruce budworm during 1983 near Hearst, Ontario. Solid line, pheromone trap catch; dotted line, predicted ovipositional curve (Régnière 1983). Standard errors are shown as lines above each mean but represent equal variation below.

minutum to parasitize spruce budworm eggs in the field. The fact that we estimated the double releases, depending upon their timing with respect to spruce budworm oviposition, to be as effective as the triple release supports their findings. When parasitoids were applied at the appropriate time in the ovipositional period, their progeny emerged from spruce budworm eggs in the field at sufficient densities to make additional releases redundant.

Effect of application rate on parasitism. Information on the relationship between rates of application and parasitism was generated by the different densities of parasitoids applied in 1982 and 1983. In 1982, following the single release of ca. 240 000 female *T. minutum* per hectare, maximum parasitism of sentinel egg masses varied between 10.3 and 18.9% (Table 2). Due to the delay and extension of emergence from the first release, these parasitoids were active at approximately the same time as those from the second release (Fig. 1*b*). Therefore, on the double release plot there was, in effect, a single release of ca. 480 000 females per hectare (Fig. 1*a*). Maximum parasitism resulting from this large single release, as estimated by sentinel egg masses, averaged 18.5%, with considerable variation between the two double release plots (SE = 6.6%). The effect of the higher release rates on parasitism is apparent from the peaks during August when maxima of 8.4 and 19.1% of the sentinel egg masses were parasitized following the release of 240 000 and 480 000 females per hectare, respectively (Fig. 1*b* and 1*a*). These peaks, ca. 20 days after the releases, represent the second generation of *T. minutum* emerging from spruce budworm eggs laid naturally in the field, and suggest that the doubling of the release rate doubled the parasitism rate of naturally laid eggs.

In 1983, at a release rate of ca. 12 million females per hectare, maximum parasitism of sentinel egg masses was 82.2% following a single early release and 91.1% following a single late release (Fig. 2*c* and Table 2). An average of 86.6% of the susceptible egg masses deposited by spruce budworm, therefore, were parasitized following the release of ca. 12 million female *T. minutum* per hectare.

An additional effect of increasing the release rate of *T. minutum* was seen when either egg parasitism (proportion of eggs parasitized per egg mass) or daily parasitism was examined. The total percentage of eggs parasitized within each discovered, sentinel egg mass was 50.1 (± 5.2)% in 1982 and 80.3 (± 2.5)% in 1983, suggesting both egg mass parasitism and egg parasitism increased when higher numbers of *T. minutum* were released.

In 1982, at ca. 360 000 females per hectare, daily parasitism of sentinel egg masses and eggs averaged 2.3 and 0.8%, respectively, but in 1983 at ca. 12 million females per hectare, daily parasitism averaged 21.2 and 15.3%, respectively (Table 2). A 33-fold increase in the application rate of *T. minutum* between 1982 and 1983, therefore, resulted in a 9-fold increase in daily parasitism of egg masses and a 19-fold increase in daily parasitism of eggs, i.e. the relationship between the rate of parasitism and the rate of release for *T. minutum* was not linear. We have reported similar results using fixed densities of parasitoids in field cages (Smith *et al.* 1986).

Effect of host egg on parasitism. In both 1982 and 1983, egg parasitism was lower immediately following the releases than when the second generation of *T. minutum* emerged from spruce budworm eggs in the field. Egg parasitism immediately after the double releases in 1982 peaked at an average of 6.2% but during the second generation in August it peaked at an average of 14.4% (Fig. 4*a*). Similarly, in 1983, egg parasitism following each release peaked at an average of 58.6% compared with 71.8% for the second generation of *T. minutum* on the triple release plot (Fig. 4*b*). This increase in parasitism of sentinel eggs later in the season may be attributed, in part, to the increase in the actual

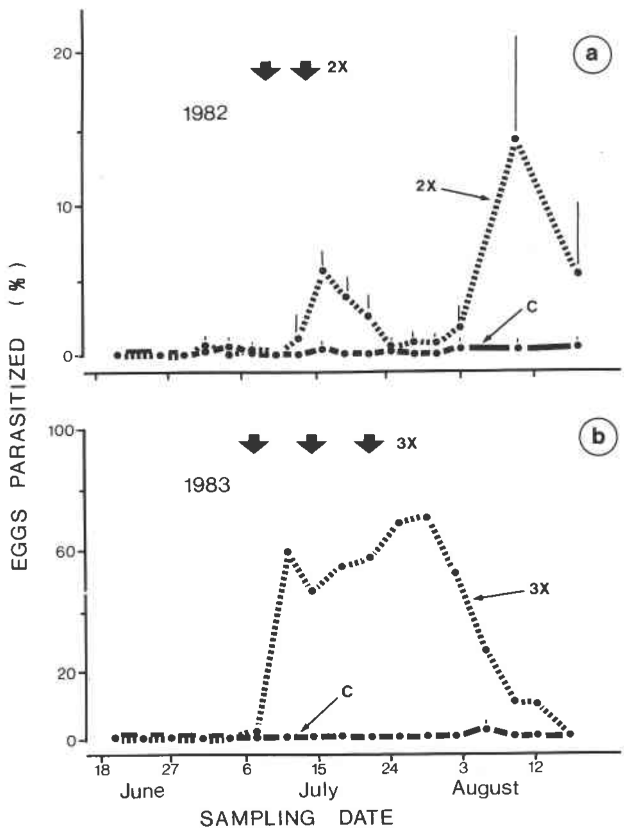

FIG. 4. Parasitism of sentinel spruce budworm eggs following ground release of *Trichogramma minutum* near Hearst, Ontario, during 1982 and 1983. Arrows indicate release dates and solid lines represent control plots. Dotted line: *a*, two double release plots of 240 000 females per hectare per release (8 and 14 July 1982); *b*, one triple release plot of ca. 12 million females per hectare per release (7, 14, and 21 July 1983). Standard errors are shown as lines above each mean but represent equal variation below.

number of parasitoids. Larger numbers of second-generation parasitoids would be present in the field at the end of the ovipositional period, having emerged from eggs laid naturally during the earlier releases.

The observed increase in parasitoid numbers on the release plots alone cannot account completely for the higher egg parasitism observed later in the season. In 1983, the single late release on 21 July coincided almost exactly with the second generation of *T. minutum* emerging from spruce budworm eggs laid during the single early release on 7 July. As was discussed previously, however, the single late release essentially missed the ovipositional period of the spruce budworm. Therefore, on the late single release plot alone (plot 6), relatively few second-generation parasitoids were present during August. Despite this, the percentage of eggs parasitized within each egg mass from the second generation of *T. minutum* on this plot averaged 81.0% and was considerably higher than the mean for the first generation of parasitoids released on all plots (i.e. 71.1%). This suggests that not only were there more parasitoids present later in the oviposition period, but also that those parasitoids emerging from spruce budworm eggs were more efficient than those emerging from eggs of the standard rearing host. The increased longevity and fecundity of *T. minutum* reared on eggs of spruce budworm compared with species of flour moth may account, partially, for this superior performance in the field (Houseweart *et al*. 1983; Smith *et al*. 1986; Smith and Hubbes 1987).

Effect of parasitism on larval populations. In 1984, on the triple release plot 3 where 58.0% of the egg masses were parasitized in 1983, only 17.4 2nd-instar larvae per square metre foliage were found compared with 88.0 2nd-instar larvae per square metre foliage found on control plot 7. This represents a significant reduction of 80.3% ($p \leq 0.05$) in larval populations. This large reduction in larval populations compared with egg mass parasitism may have been partly due to natural differences in stand condition and egg mass or stand density on the control plots.

Only one study has dealt with the effect of *Trichogramma* parasitism on host population levels of a forest insect. Kang-Jou (1980/1981) found that 96% egg parasitism by *T. dendrolimi* Mats. reduced larval populations of the pine defoliator, *Dendrolimus punctatus* Wlk., by 100%. In some pest species, it has been suggested that egg parasitism and early larval mortality could be complementary and that small fluctuations in real mortality between 90 and 100% could have a marked effect upon subsequent host populations (Van Hamburg and Hassell 1984). For insects such as the spruce budworm, natural egg–larval mortality approaches 98%, with egg parasitism accounting for ca. 10% of this mortality (Morris 1963). If we assume that overall mortality for spruce budworm is density independent, elevating rates of egg parasitism from 10 to 60% will increase mortality for that generation by only 0.25%. This slight increase in egg mortality will reduce spruce budworm populations further only if overall mortality is already 98% (Morris 1963). It is unlikely, however, that those factors influencing spruce budworm mortality act independent of budworm density. Royama (1984) considers spruce budworm populations to be regulated by second-order density-dependent factors. A 60% increase in egg mass parasitism, therefore, could lead to a significant reduction in spruce budworm populations depending upon the relationship and density-dependent strength of those mortality factors following egg parasitism.

Potential for carryover. Essentially no parasitism (0.3%) was observed in years following inundative release of *T. minutum*. The harsh winters and lack of ecological diversity in this region probably reduce the availability of alternate hosts and this would account partially for the absence in carryover (Houseweart *et al*. 1984*b*). Under such stand conditions, therefore, releases of *T. minutum* for control of the spruce budworm must only be considered inundative.

Conclusions

Inundative releases of 12 million female *T. minutum* per hectare will result in parasitism of susceptible spruce budworm egg masses in the field of ca. 87% with maximum parasitism achieved by using two separate releases, 5–7 days apart, early in the ovipositional period of the spruce budworm. In this way, a large number of parasitoids will be active 12–19 days later towards the end of the ovipositional period, providing continuous parasitism in the field without the cost of additional releases. In addition, those parasitoids emerging from spruce budworm eggs will be more efficient than those emerging from the standard rearing host and, thus, will improve parasitism in the field. If this strategy is implemented, egg mass parasitism and reductions in subsequent larval populations will be increased significantly.

The feasibility of using *T. minutum* as a biological control agent against forest pests such as the spruce budworm in Canada depends upon financial considerations and, to a large extent, upon the development of integrated forest pest management practices in general. Spruce budworm control may be enhanced by either augmenting or replacing current control programs with inundative releases of a parasitoid attacking the egg stage. If *T. minutum* were released against the egg stage, the application of insecticides to control subsequent larval populations may be greatly reduced. On the other hand, releases made after larviciding programs are completed may have a significant impact at lower host densities and retain spruce budworm populations below economic levels for several years.

Morris (1963) considered the potential of parasitoids, and in particular egg parasitoids such as *T. minutum*, for the natural control of the spruce budworm to be poor. He did not consider inundative releases of such parasitoids. The present study has demonstrated the potential of *T. minutum* when used inundatively to lower populations of spruce budworm even in areas of high density. It is not known, however, whether this level of suppression is significant enough to reduce populations of spruce budworm below damaging levels. As yet, no economic threshold for spruce budworm has been clearly defined and releases of *T. minutum* have not been tried in areas of low budworm density.

Acknowledgments

The authors thank S.A. Nicholson, M. MacCosham, J. Juswick, and FIDS for field support; J.E. Laing, G. Eden, D.S.K. Yu, and D. Whitson for production of parasitoids; D.R. Wallace, Z. Faux, K. Tomlinson, and C. Charlette for sentinel egg masses; D.R. Wallace and R. Street for loan of equipment; and D.R. Wallace, J.E. Laing, and V. Nealis for reviewing. Special thanks to J. Régnière for help with analysis and D.R. Wallace and FIDS for allowing use of unpublished data. Funding was provided through scholarships to SMS from the Natural Sciences and Engineering Research Council of Canada and the Canadian Forestry Service, and by the Ontario Ministry of Natural Resources and the Ontario Ministry of the Environment.

References

Hassan, S.A. 1982. Mass-production and utilization of *Trichogramma*: 3. Results of some research projects related to the practical use in the Federal Republic of Germany. pp. 213–218 *in* INRA Publ., 1982. *Les Colloques de l'INRA 9*.

Houseweart, M.W., D.T. Jennings, and R.K. Lawrence. 1984*a*. Field releases of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) for suppression of epidemic spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), egg populations in Maine. *Can. Ent.* **116**: 1357–1366.

——— 1984*b*. Alternate insect hosts and characteristics of forest stands supporting native populations of *Trichogramma minutum* Riley. *Misc. Rep.* 300. College of Forest Resources, Maine Agric. Exp. Stn., Univ. of Maine, Orono, USA. 32 pp.

Houseweart, M.W., D.J. Jennings, C. Welty, and S.G. Southard. 1983. Progeny production by *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) utilizing eggs of *Choristoneura fumiferana* (Lepidoptera: Tortricidae) and *Sitotroga cerealella* (Lepidoptera: Gelechiidae). *Can. Ent.* **115**: 1245–1252.

Houseweart, M.W., S.G. Southard, and D.J. Jennings. 1982. Availability and acceptability of spruce budworm eggs to parasitism by the egg parasitoid, *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). *Can. Ent.* **114**: 657–666.

Jennings, D.T., and M.W. Houseweart. 1983. Parasitism of spruce budworm (Lepidoptera: Tortricidae) eggs by *Trichogramma minutum* and absence of overwintering parasitoids. *Environ. Ent.* **12**: 535–540.

Kang-Jou, H. 1980/1981. The use of biological agents for the control of the pine defoliator, *Dendrolimus punctatus* (Lepidoptera: Lasiocampidae), in China. *Prot. Ecol.* **2**: 297–303.

Lawrence, R.K., M.W. Houseweart, D.T. Jennings, S.G. Southard, and W.A. Halteman. 1985. Development rates of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) and implications for timing augmentative releases for suppression of egg populations of *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. Ent.* **117**: 557–563.

Leius, K. 1960. Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. *Can. Ent.* **92**: 369–376.

Morris, R.F. 1963. The dynamics of epidemic spruce budworm populations. *Mem. ent. Soc. Can.* 31. 332 pp.

Oatman, E.R., and G.R. Platner. 1971. Biological control of the tomato fruitworm, cabbage looper, and hornworms on processing tomatoes in southern California, using mass releases of *Trichogramma pretiosum*. *J. econ. Ent.* **64**: 501–506.

——— 1978. Effect of mass releases of *Trichogramma pretiosum* against lepidopterous pests on processing tomatoes in southern California, with notes on host egg populations trends. *J. econ. Ent.* **71**: 896–900.

Parker, F.D., F.R. Lawson, and R.E. Pinnell. 1971. Suppression of *Pieris rapae* using a new control system: Mass releases of both the pest and its parasites. *J. econ. Ent.* **64**: 721–735.

Régnière, J. 1983. An oviposition model for the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. Ent.* **115**: 1371–1382.

Ridgway, R.I., J.R. Ables, C. Goodpasture, and A.W. Hartstack. 1981. *Trichogramma* and its utilization for crop protection in the U.S.A. Proc. Joint Am.–Soviet Conf. on Use of Beneficial Organisms in the Control of Crop Pests. Ent. Soc. Am., Coll. Pk., MD, USA.

Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecol. Monogr.* **54**(4): 429–462.

Sanders, C.J. 1980. A summary of current techniques used for sampling spruce budworm populations and estimating defoliation in eastern Canada. *Can. For. Ser. Rep.* O-X-306. 33 pp.

——— 1981. Release rates and attraction of PVC lures containing synthetic sex attractant of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. Ent.* **13**: 103–111.

Smith, S.M. 1984. Feasibility of using the egg parasitoid, *Trichogramma minutum* Riley, for biological control of the spruce budworm. Ph.D. thesis, University of Toronto. 221 pp.

Smith, S.M., and M. Hubbes. 1987. Isoenzyme patterns and biology of *Trichogramma minutum* as influenced by rearing temperature and host. *Entomologia exp. appl.* In press.

Smith, S.M., M. Hubbes, and J.R. Carrow. 1986. Factors affecting inundative releases of *Trichogramma minutum* against the spruce budworm. Proc. Symp. *Trichogramma*, XVII Int. Cong. Entomol., Hamburg, FDR. *Z. ang. Ent.* **101**: 29–39.

Stinner, R.E. 1977. Efficacy of inundative releases. *Annu. Rev. Ent.* **22**: 515–531.

Van Hamburg, H., and M.P. Hassell. 1984. Density dependence and the augmentative release of egg parasitoids against graminaceous stalkborers. *Ecol. Ent.* **9**: 101–108.

Walter, V.S. 1983. Biological and ecological studies on egg parasites from the genus *Trichogramma* Westwood (Hymenoptera: Chalcidoidea). Part I: Investigations carried out in selected forest biocoenoses in the GDR. *Zool. Jb. Syst.* **110**: 271–299.

(Date received: 1986 05 05; date revision received: 1986 09 22; date accepted: 1986 11 03)