Pattern of Attack on Spruce Budworm Egg Masses by *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) Released in Forest Stands

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ABSTRACT Female *Trichogramma minutum* Riley released from a central point in a white spruce, *Picea glauca* (Moench) Voss, plantation attacked eggs of the spruce budworm, *Choristoneura fumiferana* (Clemens), locally around the point of release. Dispersion parameters showed an aggregated pattern of attack—mean ($\bar{m}$), 1.6 parasitized egg masses per station; mean index of crowding (m^*), 20.5; Lloyd's index of patchiness (IP), 7.3. Parasitoids dispersed a total distance of 18.5 m over 5 d, with a mean horizontal distance ($\hat{d}$) of 4.3 ± 0.2 m and an average dispersal rate of 7.2 cm/h. Movement by *T. minutum* within trees was not affected by wind; however, dispersal between trees during the first 2 d after release tended to be downwind. Average vertical distance of dispersal within trees from a point 0.25 m above ground was 2.4 m (±0.05 m). When *T. minutum* was released at this height in 1984, parasitism of egg masses was significantly higher at 3.25 m above ground than at 2.25 or 1.25 m above ground. The reverse was true when parasitoids were released at ground level. Greater parasitoid movement was seen on jack pine, *Pinus banksiana* Lamb., than on white spruce. Dispersal by female *T. minutum* was influenced by stand complexity and volume.

KEY WORDS Insecta, dispersal, parasitism, *Choristoneura*

INUNDATIVE RELEASES of the egg parasitoid *Trichogramma minutum* Riley have potential for suppressing outbreak populations of the spruce budworm, *Choristoneura fumiferana* (Clemens) (Smith et al. in press). The ability of parasitoids to locate hosts effectively determines their success as biological control agents. Therefore, to assess the feasibility of using inundative releases for control of the spruce budworm, it is necessary to examine the pattern of attack and movement of female *T. minutum* under forest conditions.

After release in agricultural crops, species of *Trichogramma* disperse horizontally from 30.5 to 1,610 m (Jaynes & Bynum 1941, Stern et al. 1965, Stinner et al. 1974). Vertical movement in apple orchards is also variable—Stein (1961) reported greater parasitism by *T. embryophagum cacoeciae* (Hartig) in the upper canopy of apple trees, whereas Yu et al. (1984) found the frequency of attack by *T. minutum* to be greater in the lower canopy. In general, *T. minutum* is an arboreal species (Fye & Larsen 1969, Thorpe 1984–1985) which parasitizes species of *Choristoneura* to a greater extent in the middle to upper crown of trees than in the lower crown (Kemp & Simmons 1978, Schmidt 1981, Jennings & Houseweart 1983, Houseweart et al. 1984).

The rate and extent of movement into the forest canopy by *T. minutum* following inundative releases has not been studied, nor have those factors such as wind direction, which may affect dispersal. The present study was conducted to examine the spatial and temporal pattern of attack by field-released female *T. minutum* on egg masses of spruce budworm and to relate these patterns to the successful use of this parasitoid in inundative releases.

Materials and Methods

The attack pattern of female *T. minutum* on spruce budworm was examined in release–resultant parasitism experiments. Laboratory-reared parasitoids were released at a central point in forest stands where sampling by the Forest Insect and Disease Survey, Canadian Forestry Service, indicated low levels of natural *T. minutum*. Dispersal was estimated by measuring the parasitism that resulted in sentinel egg masses. Sentinel egg masses (<48 h old) were laid in the laboratory on balsam fir, *Abies balsamea* (L.) Mill., foliage by spruce budworm reared on an artificial diet (Smith et al. in press). These egg masses were placed in the field at designated locations and changed daily to ensure a continuous supply of susceptible eggs. Egg masses retrieved from the field were kept in individual gelatin capsules until the number of parasitized

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(blackened) egg masses and eggs per egg mass could be determined for each date, height above ground, distance, and direction.

Parasitoids were obtained from a colony initiated in 1981 from 10 spruce budworm egg masses collected in Plummer Township, Ontario (46°N, 84°W). They had been maintained by the Biological Control Laboratory, University of Guelph, Guelph, Ont., on eggs of the Angoumois grain moth, *Sitotroga cerealella* (Olivier) from 1983 to 1985. During this period, the parasitoid colony was infused annually with field-collected *T. minutum* and kept in continuous culture between 1983 and 1985 (26–104 generations) at 25°C, 75% RH, and 16:8 (L:D) photoperiod.

Dispersal in a Plantation. Dispersal of *T. minutum* from a single point source was studied in 1983 and 1984 near Hearst, Ont. (50°N, 84°W) in a 12- to 20-yr-old white spruce plantation with a severe spruce budworm infestation (approximately 30 egg masses/m^2 foliage). Egg parasitism by native *T. minutum* was less than 3% in this area (Smith et al. in press). The plantation had a stand density of 2,430 trees/ha and consisted of 26% white spruce, *Picea glauca* (Moench) Voss, 65% balsam fir, 6% poplar, *Populus* spp., and 3% white birch, *Betula papyrifera* Marsh.

Six sentinel egg masses were attached to each of 17 white spruce trees. The sample trees averaged 6.7 ± 0.3 m ($\bar{x}$ ± SE) in height, had a diameter at breast height (dbh) of 9.3 ± 0.6 cm, and exhibited 10% defoliation as a result of spruce budworm. The 17 trees were arranged in the shape of a cross, with the arms of the cross oriented north–south and east–west. There were four trees per arm of the cross, one tree at the center, and the spacing between trees was 5 m. Within each tree, egg masses were arranged so that there were two egg masses (one on either side of the tree) at each of three different heights in the canopy—1.25, 2.25, and 3.25 m above ground. Sentinel egg masses were changed daily from 10 to 19 August 1983 and from 19 July to 5 August 1984. This design allowed examination of *T. minutum* movement along a transect (horizontal dispersal) as well as within the canopy (vertical dispersal) for each day following release.

Parasitoids were sent to the study site in host eggs attached to cards (10 by 15 cm) that had been sprayed with distilled water. For each release, one card was folded and placed inside a triangular paper cup (volume approximately 150 ml) with openings at both top and bottom to permit escape of the parasitoids. Each cup was then pinned to a stake 0.25 m above ground directly beneath the central sample tree. A small sample (500 parasitized eggs) was retained in a field laboratory to assess the extent of parasitoid emergence and the sex ratio in emergent populations. The number released was estimated from the number of parasitized eggs per card and the percentage of females emerging from these samples. Approximately 115,000 female *T. minutum* were released on 12 August 1983; approximately 169,000 and 119,000 female *T. minutum* were released on 26 and 31 July 1984, respectively. During both years, weather conditions were recorded hourly at a meteorological station 15 km from the release site.

Dispersal within Individual White Spruce and Jack Pine. In 1985, experiments on dispersal of female *T. minutum* were conducted in two small (<0.5 ha) 7- to 10-yr-old pure plantations of white spruce and jack pine, *Pinus banksiana* Lamb., near Sault Ste. Marie, Ont. (46°N, 84°W). These stands had no natural infestations of either budworm species, *Choristoneura pinus pinus* Freeman or *C. fumiferana*. Results of a prerelease study indicated that parasitism of sentinel egg masses due to naturally occurring parasitoids was less than 0.5% daily. Ten sample trees were selected, four in the white spruce plantation and six in the jack pine plantation. The average height of white spruce was 2.9 ± 0.2 m and of jack pine, 2.6 ± 0.2 m. Crown width at upper, middle, and lower canopies for white spruce was 0.9, 1.5, and 1.5 m and for jack pine, 0.7, 1.3, and 1.5 m, respectively. Sample trees were separated from each other by a minimum of 5 m and foliage contact between adjacent trees was eliminated.

Sentinel egg masses were placed on all sample trees in the upper, middle, and lower canopies at 2.5, 1.6, and 0.7 m on white spruce and at 2.2, 1.5, and 0.7 m on jack pine. Eight egg masses were tied to branches at each height, two in each cardinal direction from the central trunk. One of these two egg masses was placed adjacent to the trunk on each branch, and the other was tied to the distal end of the same branch, averaging 0.47, 0.73, and 0.75 m from the trunk at upper, middle, and lower canopies on white spruce and 0.37, 0.67, and 0.77 m, respectively, on jack pine. To monitor the day-to-day attack pattern of female *T. minutum* within each tree species, sentinel egg masses were changed daily from 12 to 27 September 1985.

Parasitoids were transported to the field as pupae in parasitized *S. cerealella* eggs but were not attached to cards. A small sample (about 200 parasitized eggs) was retained in the laboratory to assess percent emergence and the sex ratio of the emergent population. For each sample tree, 22,900 female *T. minutum* were released on 15 September 1985 by sprinkling the unattached parasitized eggs uniformly on the ground around the base of each tree. Weather conditions were monitored at a meteorological station 1 km from the study site.

Data Analysis. Because levels of natural parasitism were less than 3% in both study areas (Smith et al. in press), parasitism of sentinel egg masses was considered to result directly from the point releases. Arcsine transformations were performed on all percentage data before analysis. Analysis of variance (ANOVA) and a χ^2 test for proportions with binomial distribution (df = 1) were used to analyze differences in the frequency of eggmass parasitism between the species of host tree, direc-

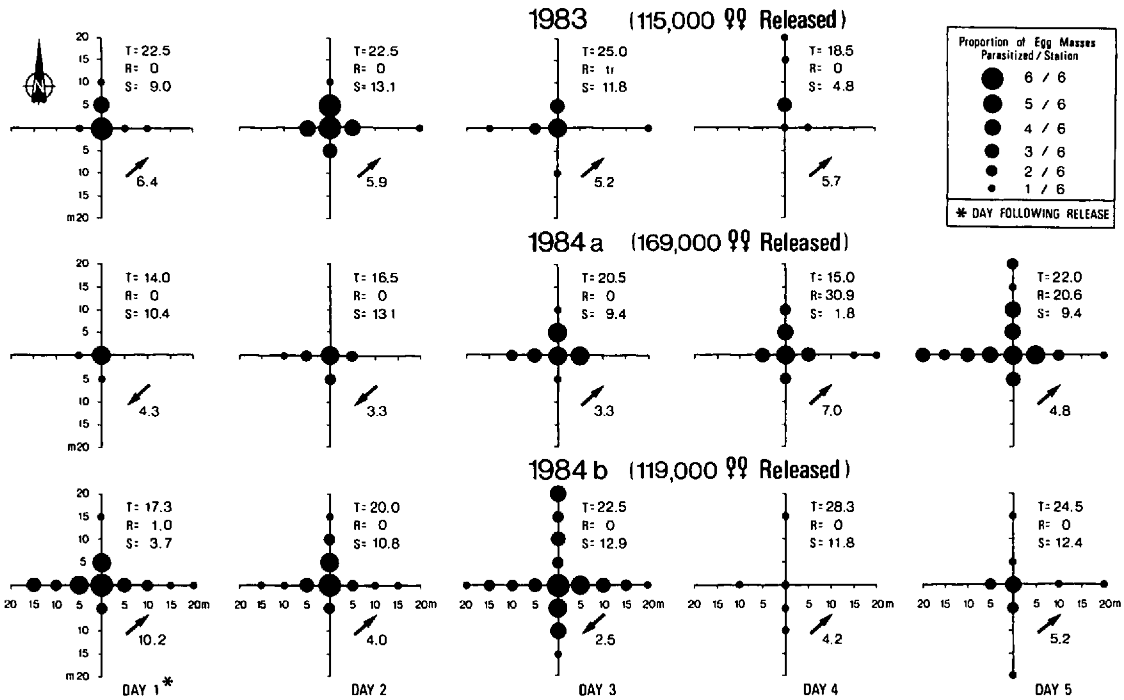

Fig. 1. Proportion of egg masses parasitized at intervals of 5 m in each cardinal direction on successive days following the release of *T. minutum* from a central point in a white spruce plantation near Hearst, Ont., in 1983 and 1984. T, temperature (°C); R, rainfall (mm); S, sunshine (h); and wind direction and speed (km/h).

tion, within-tree height, and between tree distance. For each release in 1983 and 1984, the mean and standard error of the distance ($\hat{d}$) traveled (Fletcher 1974), the cumulative distance traveled, and the rate of dispersal ($[d_{i+1} - d_i]/t$ where t is time [24 h]) were determined. The dispersion pattern of female *T. minutum* was obtained from the mean number of egg masses parasitized per station ($\bar{m}$), the index of mean crowding

$$\left(m^* \text{ where } m^* = m + \frac{s^2}{\bar{m}} - 1\right)$$

and the calculation of Lloyd's index of patchiness (IP) (Lloyd 1967).

Results

Dispersal in the Plantation. The patterns of parasitism that were observed indicate that the parasitoids dispersed from the point of release (Fig. 1). In both years, the number of parasitized egg masses decreased with increasing distance from the center of the plot. Over a 5-d period, significantly more samples within 5 m of the release site were parasitized (in 1983, 24% of 233; in 1984a, 52% of 145; in 1984b, 48% of 147) compared with parasitism 10–20 m away (3% of 551, 3% of 348, and 7% of 355, respectively) ($\chi^2 = 50.90$; df = 1; $P < 0.01$) (Table 1). On average, female parasitoids released from the point source moved a horizontal distance of 4.3 m (±0.2 m, n = 1,396). Fig. 2 shows the mean distances ($\hat{d}$) traveled by dispersing female *T. minutum* on each day following release in 1983 and 1984. In general, movement by female parasitoids was rapid during the first 24 h after release and then declined gradually over the next 4 d.

Dispersal and dispersion parameters for female *T. minutum* released from a point source are summarized in Table 1. The daily rate of dispersal decreased over time, averaging 7.2 cm/h over 5 d for all three releases. Weather conditions during the first release in 1984a (Fig. 1) may account for the comparatively low dispersal rates observed during this release. In 1984, weather during the period from the first release (1984a) to 5 d after release was cooler and wetter than for the corresponding mean periods during the other two releases (1983, 1984b) and there were fewer hours of sunshine (17.6 versus 22.3 ± 1.2°C, 10.3 mm of rain versus 0.1 ± 0.1 mm, and 8.8 h of sun versus 10.0 ± 0.4 h). Although Schmidt & Smith (1985) demonstrated that females of *T. minutum* continue to parasitize in total darkness, the extent of host searching in the absence of light is unknown for *Trichogramma*. Biever (1972) found the rate of search by *T. minutum* to be highly dependent on air temperature, suggesting that this may be the more important factor in the observed reduction of movement.

Daily values of m, m^*, and IP all suggested a highly clumped pattern of dispersion (Lloyd 1967) for female *T. minutum*: $m^* > m$ and IP > 1, with

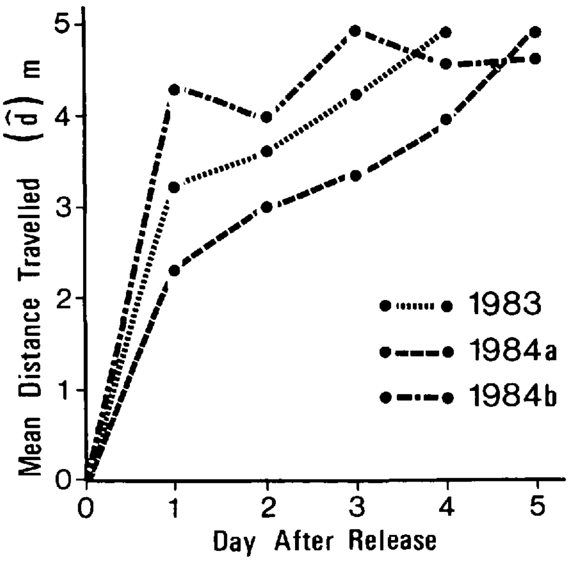

Fig. 2. Mean total distance traveled ($\hat{d}$) on successive days by female *T. minutum* released from a central point in a white spruce plantation near Hearst, Ont., in 1983 and 1984.

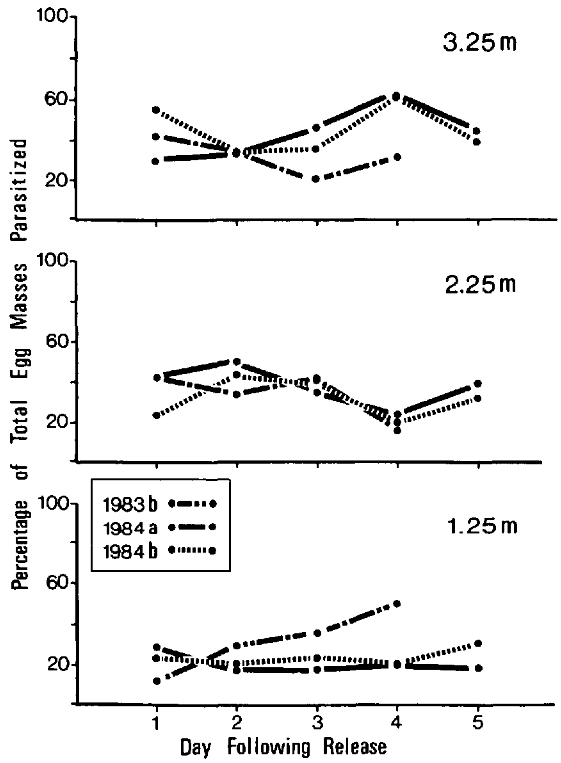

Fig. 3. Percentage of spruce budworm egg masses parasitized at each height in the canopy on successive days following the release of *T. minutum* in white spruce plantations near Hearst, Ont., in 1983 and 1984.

the degree of aggregation declining over time and becoming more random. An aggregated pattern of attack by female *T. minutum* was indicated by the observed values: *m*, 1.6 parasitized egg masses per station; *m**, 20.5; and IP, 7.3 (Table 1).

To a limited extent, wind direction appeared to influence movement by female *T. minutum* in the plantation. During 1983, the wind averaged 5.4 km/h and was predominately from the southwest. In that year, significantly more egg masses (33) were parasitized north and east of the release point than south and west (14) of the point (χ^2 = 7.16; df = 1; $P < 0.01$) (Fig. 1). In 1984a, a significantly higher rate of parasitism (χ^2 = 3.91; df = 1; $P < 0.05$) was initially observed downwind of the release point than was observed upwind. When the wind shifted and came from the southwest, parasitism was observed north and east of the release point. The effect of wind direction during the second release in 1984b, however, was less apparent, with dispersal exhibiting a diffuse pattern.

The average vertical distance ($\hat{d}$) traveled by *T. minutum* released at 0.25 m above ground level was 2.4 ± 0.05 m. Fig. 3 shows the daily percentage of parasitism at three different heights in the canopy. Overall, parasitism of sentinel egg masses was significantly higher in the upper canopy (3.25 m) than in either lower canopy level (2.25 or 1.25 m) (F = 4.21; df = 2, 507; $P < 0.05$). For both years, the percentage of eggs parasitized within each egg mass ($\bar{x}$ ± SE) was not significantly different between the three canopy heights (80.2 ± 4.61% at 3.25 m, 83.2 ± 5.35% at 2.25 m, and 72.6 ± 3.78% at 1.25 m). During 1984, parasitism at 1.25 m remained relatively constant throughout the 5 d after release (24.4 ± 2.63%). In both years, parasitism at 2.25 m averaged 34.9 ± 2.74% and declined steadily from 36.3% on day 1 to 20.3% on day 4. Although parasitism of egg masses at 3.25 m was greatest overall ($\bar{x}$, 41.0 ± 3.13%), it varied considerably from day to day and between the 2 yr.

Dispersal Within Individual White Spruce and Jack Pine. For all parameters examined (i.e., within-tree direction, distance, and height) following arcsine transformation, significantly more egg masses were parasitized by *T. minutum* in jack pine (175 out of 1,083, or 16%) than in white spruce (68 out of 608, or 11%) (χ^2 = 7.83; df = 1; $P < 0.05$). For 12 d after release on 15 September, the wind blew from the east ($\bar{x}$, 13.4 km/h), but this did not affect the direction in which the sentinel egg masses were parasitized in either tree species (Table 2). Significant differences were observed only in horizontal and vertical movements by *T. minutum* within trees; more egg masses were parasitized at the proximal ends of the branches (i.e., adjacent to the trunk) than at the distal ends (χ^2 = 5.17; df = 1; $P < 0.01$). In contrast to dispersal in the plantation, in which more egg masses were parasitized in the upper canopy than the lower canopy on 12- to 20-yr-old white spruce, more egg masses were parasitized in the lower canopy than in the upper canopy on both individual white spruce and jack pine (χ^2 = 70.42; df = 1; $P < 0.01$).

Table 1. Parameters of dispersal and dispersion for female *T. minutum* released from a central point in a white spruce plantation near Hearst, Ont., in 1983 and 1984

Year	Release date	No. released	Day following release	n^a	Distance ($\hat{d}$) traveled (m)	Daily rate of dispersal (cm/h)[b]	$\tilde{m}$	m^*	IP
1983	12 August	115,000	1	14	3.2	13.3	1.9	33.3	17.0
			2	25	3.6	7.5	2.3	35.4	15.3
			3	13	4.2	5.9	1.7	25.1	14.8
			4	6	4.9	5.1	0.5	1.2	4.4
1984	26 July	169,000	1	7	2.3	9.6	1.3	23.8	14.9
			2	12	3.3	6.4	1.6	23.0	9.7
			3	22	3.6	4.6	2.2	30.2	6.7
			4	21	5.4	3.5	2.1	27.5	6.7
			5	39	4.9	3.3	3.1	34.8	3.9
	31 July	119,000	1	31	4.3	18.1	2.9	40.9	5.2
			2	25	4.0	8.3	2.5	37.2	6.3
			3	46	4.9	6.8	3.8	45.6	3.5
			4	5	4.5	5.1	0.5	0.7	4.8
			5	13	4.7	3.8	1.5	2.7	1.9
Mean		134,333		—	4.3	7.2	1.6	20.5	7.3

[a] n, number of egg masses parasitized.
[b] Daily rate of dispersal = $\Sigma(\hat{d}_{i+1} - \hat{d}_i)/t$; $\tilde{m}$, true mean number of egg masses parasitized per station; m^*, index of mean crowding; IP, Lloyd's index of patchiness.

Discussion

Forest stands form relatively continuous foliage environments with large, complex surface areas and volumes. Such environments are comparatively more stable in time and in space than are agricultural crops. This stability will influence the behavior and movement of *Trichogramma* upon release.

Table 2. Parasitism of spruce budworm egg masses, categorized by direction, position on branch, and height above ground following release of *T. minutum* from a point at the base of either white spruce or jack pine near Sault Ste. Marie, Ont., in 1985

Within-tree parameters[a]	White spruce		Jack pine	
	n^b	Parasitism (%)[c]	n^b	Parasitism (%)[c]
Direction:				
N	146	15.8a	216	16.2a
S	146	13.7a	216	19.4a
E	146	15.1a	216	19.4a
W	146	17.1a	216	19.9a
Branch distance:				
Proximal	288	19.1a	432	23.4a
Distal	288	12.2b	432	15.3b
Height (m):				
Crown tip	24	0a	36	13.9a
2.5	192	9.4b	298	14.4a
1.6	192	14.6b	298	16.8a
0.7	192	23.4c	298	24.5b

Untransformed means followed by the same letter within each column and parameter are not significantly different at $P < 0.01$ (χ^2) test for proportions with binomial distributions (Ostle & Mensing 1975).
[a] Mean weather data for 12 d following release on 15 September 1985: temperature, 14.5°C; rainfall, 2.1 mm; sunshine, 5.1 h; wind speed and direction, 13.4 km/h E.
[b] Represents total number of sentinel egg masses exposed daily over 6 d for each parameter.

Smith (1984) suggested that female *T. minutum* were capable of moving 10 to 20 m outside plots that received uniform applications of 120,000 females/ha. In the present study, the spatial pattern of attack by female *T. minutum* within and between trees was localized near the point of release. When released at ground level, females moved upward near the tree trunks, parasitizing a greater number of egg masses next to the trunk than on the branch tips. Regardless of the species of host tree, oviposition activity also tended to be concentrated in the lower canopy closer to the release point. When parasitoids were released on relatively open areas at a height of 0.25 m above ground level (i.e., not directly at the base of the sample tree), the distribution of egg parasitism was reversed—the parasitoids moved only a short distance into the upper canopy, where the majority of host eggs are laid (Morris 1963). Similar distributions (i.e., in the upper canopy) have been reported after the broadcast release of the parasitoid (Smith 1984, Smith et al. 1986).

The direction of the prevailing wind appeared to have an effect on the early between-tree movement of female *T. minutum*. Other authors have reported on the effect of wind direction on parasitoid distribution (Jaynes & Bynum 1941, Stein 1961, Hendricks 1967, Yu et al. 1984). Hendricks (1967) hypothesized that wind could hamper the ascent or descent of *T. minutum* through plant canopies. In the present study, upward movement within trees was apparently uninfluenced by wind direction or speed, possibly because the volume of foliage on individual trees interrupted air movement. Further microclimatic studies are needed to investigate the extent of local wind disruption.

The high volume of foliage in forest stands effectively reduces the speed and distance of searching by female parasitoids. Movement along horizontal transects in the white spruce plantation took place at approximately 7.2 cm/h, with an average dispersal distance of 4.3 m over 5 d. In agricultural crops such as cotton, cabbage, and alfalfa, the rate of dispersal by *Trichogramma* species is considerably greater, ranging from 2.5 m/h (Stinner et al. 1974) to 35.8 m/h (Stern et al. 1965). In the present study, the estimated surface area each female *T. minutum* would be required to search upon emergence to find an egg mass was approximately 4,600 cm^2. Need & Burbutis (1979) defined 2,800 cm^2 of leaf surface as one searching unit for *T. nubilale* on corn plants, whereas Burbutis & Koepke (1981) demonstrated an inverse relationship between plant size and parasitism. This suggests that the increased volume of foliage in forest stands will require higher numbers of *Trichogramma* to be released to achieve the same level of parasitism than would be expected in agricultural crops.

Fye & Larsen (1969) have shown that the searching capability of female *Trichogramma* is seriously hampered by complexity of the foliage environment. In the present study, the effect of foliage complexity on the attack pattern of female *T. minutum* was demonstrated by the difference in egg mass parasitism between jack pine and white spruce. Overall, parasitism in jack pine was greater than that in white spruce, with egg masses being parasitized on the crown tips of jack pine but not of white spruce. Foliage of jack pine is relatively sparse compared with that of spruce, particularly in trees 7–10 yr of age, and this would allow for greater movement by female parasitoids. Such an observation suggests that, under similar stand conditions, fewer *T. minutum* might be required for the same degree of control of jack pine budworm than would be required to control spruce budworm.

The practical implication of this study is that uniform applications of *T. minutum* in forest stands will be achieved only if inundative releases are made on localized sites with consideration given to the initial direction of the wind. Although some female parasitoids will disperse more than 20 m horizontally in these forest stands, a significant number move less than 5 m, and only their initial direction of movement may be affected by wind direction. Vertical movement within the canopy (both rate and extent) will not be affected by wind but instead will be affected by the density and complexity of the trees and their foliage. For more mature stands, the parasitoids will live long enough (i.e., 9–10 d, see Smith et al. [in press]) when released at ground level to disperse into the upper canopy where the majority of host egg masses are laid. This within-crown movement will improve egg mass parasitism and provide more effective control of the host insects. Research should concentrate on these areas because such factors could significantly affect the approach to future releases of *Trichogramma* in forestry.

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