ESTIMATED EGG DEPOSITION BY INVADING SPRUCE BUDWORM MOTHS (LEPIDOPTERA: TORTRICIDAE)

C. A. MILLER, D. O. GREENBANK, and E. G. KETTELA
Canadian Forestry Service, Maritimes Forest Research Centre,
Fredericton, New Brunswick E3B 5P7

Can. Ent. 110: 609–615 (1978)

Abstract

A 4000-ha block of spruce budworm, *Choristoneura fumiferana* (Clem.), infested forest in western New Brunswick was sprayed repeatedly in 1975 during the larval stage of budworm development. The objective was to reduce the population of the 1975 generation to a minimum level so that most of the following generation eggs found on the block could be attributed to invading females, thus providing data on the impact of moth invasion.

The presence of dispersing adults in the airspace over the block was monitored by a ground-based radar unit while light traps and pheromone-baited traps were used to confirm that invasion had taken place. A total egg population of 33.8 masses per m^2 of foliage was found on the block and indirect estimates suggest that invading females deposited about 10 of these masses.

Résumé

Un bloc de 4 000 ha de forêt infestée par la Tordeuse des bourgeons de l'Epinette, *Choristoneura fumiferana* (Clem.) au Nouveau-Brunswick a été arrosé à maintes reprises en 1975 durant le stade larvaire de la Tordeuse. L'objectif visé était de réduire au minimum la population de la génération de 1975, afin que la plupart des oeufs de la génération suivante puissent être attribués aux femelles envahissantes, fournissant ainsi des données sur l'influence de l'invasion des papillons.

La présence des adultes se dispersant dans l'espace aérien au-dessus du bloc a été suivie de près par une unité radar pendant que des pièges lumineux et à phérormones étaient utilisés pour confirmer l'invasion. Une population totale d'oeufs à raison de 33.8 masses par m^2 de feuillage fut relevée dans ce bloc et des évaluations indirectes ont supposé que les femelles envahissantes avaient pondu environ 10 de ces masses.

Introduction

The dispersal of adult spruce budworm, *Choristoneura fumiferana* (Clem.), is a known phenomenon (Greenbank 1957, 1963), but the effect of this invasion on egg-mass densities in invaded sites has not been documented in a quantitative manner. Greenbank (1973) showed that emigrating females carry about 50% of their egg complement and thus invading females could play a critical role in triggering an outbreak, spreading an on-going outbreak, and repopulating areas treated in budworm control operations. Conversely, emigration from non-favorable sites could contribute to the collapse of an infestation.

In 1975, a joint program was developed in New Brunswick by the Provincial Department of Natural Resources, Forest Protection Ltd., J. D. Irving Ltd., and the Maritimes Forest Research Centre to determine the impact of moth invasion on the repopulation of areas treated in larval spraying operations. The information would help to explain the dynamics of dispersal, and aid in the development of strategies to suppress populations through adult spraying (Miller *et al*. 1973).

Methods

The design of the experiment was to apply multiple sprays to one 4000-ha test block to reduce the level of the resident budworm larval population so that the eggs found in the block could be classified as deposition by invading females. The experimental block was in west-central New Brunswick within an area designated for maximum protection in the 1975 operational spray plan and therefore, in theory, would have few surviving budworms. Ten plots (T1–T10) were established within the 4000-ha test block. Nine plots (P1–P9) were selected on the periphery of the test block but within the operational spray zone. Three control plots (C1–C3) were in a nearby unsprayed forest. Five balsam fir (*Abies balsamea* L. Mill.), and five spruce, red (*Picea rubens* Sarg.), or red-black hybrid (black, *Picea mariana* (Moench) Voss.), were selected as sample trees in each plot. The number of trees and tree diameters were used in the test block to determine the amount of foliage per hectare (Morris 1955, fig. 16). Populations per hectare could then be estimated by counting the number of budworm on sample branches. The number of pupae, egg masses, and overwintering larvae counted on one whole mid-crown branch per tree and numbers were expressed per m^2 of foliage.

Adult activity and abundance were monitored by radar (Schaefer 1976), light traps, and sticky traps baited with the major component of the budworm female pheromone (Weatherston *et al*. 1971). The ground-based radar unit was set up in a clearing on the western border of the test block and was operated nightly from 4 July to 21 July to determine the density of moths in the airspace over the test block. Two light traps, one suspended within the forest canopy of the test block, the other in a clearing at the edge of the block, were used to confirm that moths observed in the airspace did, in fact, land in the test block. It is suspected that most dispersing budworm moths settle in forest areas at the end of their dispersal flight but some will, by chance, come down in clearings and wait until morning before moving into surrounding forests. Thus, a light trap in a clearing may pick up moth invasion.

A total of 25 pheromone traps was placed in the test block on 25 June to obtain an index of male moth abundance. These traps were checked and replaced daily until 24 July.

Early oviposition trends were determined by washing sample branches in boiling water to remove the unhatched masses. The final egg-mass counts were determined by visual examination of the foliage.

Results

Suppression of Resident Populations in the Test Block

Random samples of balsam fir in all study plots in early June showed an average pre-spray population of over 400 third- and fourth-instar larvae per m^2 of foliage. Between 3 June and 22 June, the operational spray area received a series of treatments that reduced the number of budworm to about 17 sixth-instar larvae per m^2 of foliage. The test block then received one additional treatment. The number of surviving pupae in early July was 2.97/m^2 foliage on plots T1–T10 in the test block, 6.06/m^2 on plots P1–P9, and 29.7/m^2 on the unsprayed control plots (Table I). The pupal populations were higher on red-black spruce. Laboratory rearings gave a pupal survival of 90% on all sprayed blocks; 47% of the adults were females. The number of female moths per hectare was estimated from these data (Table I). The data on number of trees per hectare and tree diameters on the test block, though limited, showed a branch surface area of 43,000 m^2/ha of balsam fir and 29,000 m^2/ha of spruce. Thus, the estimated number of female moths in the test block was (43,000) (1.26) = 54,000 on fir and (29,000) (2.47) = 72,000 on red-black spruce or a total of 126,000 females/ha. This was a surprisingly high population in view of the repeated larval sprayings.

Monitoring Moth Invasion

Radar can be used to distinguish a moth in the airspace (based on size of echo and wing-beat frequency), determine a height-population density relationship, and indicate the speed and direction of flight (Schaefer 1976). On the 6/7, 7/8, and 8/9 July, radar observations over the test block showed the number of moths of both sexes in the airspace exceeded 10,000/ha (Table II), a density we consider to be a significant 'presence'. Thus, the radar counts showed a probability of invasion on these three nights. There may also have been large numbers of moths in the airspace on two more nights: 4/5 and 12/13 July. On the 4/5 July, rain forced the early shutdown of the monitoring unit. On the 12/13 July, a rapid drop in budworm numbers preceded the shutdown of the unit at 0100 h, but it was learned later from light trap data that moth activity peaked after the shutdown.

The counts of moths in the light trap in the clearing did not correspond precisely with the radar counts. Sudden increases in the number of budworm coupled with a high proportion of budworm in the total catch were recorded in the clearing trap on the nights 4/5, 8/9, and 12/13 July (Table II). A moderate catch was recorded on the 6/7 July. These data are interpreted as budworm invasions on 4/5, 6/7, 8/9, and 12/13 July. The radar counts (Table II) suggest that a sufficient number of moths were available on two of these nights, 6/7 and 8/9 July, to indicate an invasion. However, radar counts of fewer than 5000 moths/ha on 4/5 and 12/13 July gave little indication that over 2000

Table I. Number of pupae and egg masses per m^2 of foliage in the test block (T), surrounding spray zone (P), and unsprayed plots (C)

	Pupae + pupal cases/m^2		
Plot	Balsam fir	Red-black spruce	Egg masses/m^2 on fir
T 1	0.0	0.00	17.7
T 2	0.0	0.00	31.4
T 3	3.12	20.8	72.1
T 4	0.54	3.34	60.3
T 5	5.25	–	73.2
T 6	1.48	12.5	39.8
T 7	2.30	2.60	16.6
T 8	0.66	1.77	37.6
T 9	8.63	10.4	33.1
T10	7.69	1.19	50.4
Plot mean	2.97	5.84	43.2
Calculated no. of females	1.26	2.47	
P1	9.03	8.03	21.3
P2	2.20	22.3	25.8
P3	15.9	9.28	15.8
P4	2.35	15.5	11.9
P5	2.01	4.50	20.9
P6	8.46	7.88	6.97
P7	3.87	2.88	38.1
P8	1.69	5.69	47.8
P9	9.01	18.0	54.5
Plot mean	6.06	10.5	27.0
Calculated no. of females	2.56	4.4	
C1	56.6	–[a]	79.3
C2	20.9	–	24.7
C3[b]	11.7	–	18.2
Plot mean	29.7		

[a]No data.
[b]Possibly received spray drift.

https://doi.org/10.4039/Ent110609-6 Published online by Cambridge University Press

moths could be taken each night in a clearing light trap. Conversely, the count of 45 moths in the clearing light trap on the 7/8 July gave no indication that 30,000 moths were in the airspace over the study area.

We believe these discrepancies between radar and clearing light trap counts can be explained. On 4/5 and 12/13 July, there was an early shutdown of the radar and, therefore, maximum moth densities in the airspace were not measured. On the 7/8 July, the large numbers of moths observed on radar were still airborne at 0300 h, about 1.5 h before first light. This would leave little time for invaders to respond to the light trap and could account for the low catch. Thus, we suspect that five invasions took place but neither the radar nor the clearing light trap provided an infallible detection of these invasions.

A light trap within the crown canopy of a budworm-infested stand will generally catch a large number of male and partially-spent female moths each night—both residents and invaders. High catches were recorded from 6 July to 12 July in the canopy light trap in the test block (Table II). It is difficult to pick out invasion nights from these data. Nevertheless, it could be argued that catch increases from 90 to 1750 on 4/5 July

Table II. Nightly counts of budworm moths in or near the test block based on radar, light traps, and pheromone traps

	Radar	Light traps			Pheromone trap
		In clearing		In canopy	
Night of	Estimated peak no. of moths/ha	No. of budworm	% budworm in total catch	No. of budworm	Mean male catch/trap
25/26 June					0
26/27					0.4
27/28					11.5
28/29					17.4
29/30					17.2
30/1 July					24.6
1/2					20.2
2/3					23.0
3/4		2	22	90	23.8
4/5	(3,880)*	2870	95	1750	31.4
5/6	3,740	2	9	205	27.1
6/7	11,860	529	73	3480	42.6
7/8	29,950	45	29	2810	42.1
8/9	15,220	1871	85	6630	32.2
9/10	1,180	8	12	4340	26.8
10/11	105	169	44	2380	21.3
11/12	1,370	15	14	1590	15.4
12/13	(1,235)	2592	80	2220	35.4
13/14	80	5	11	870	16.9
14/15	645	0	0	1660	12.9
15/16	45	6	11	22	14.0
16/17	55	50	3	850	23.8
17/18	75	120	9	1160	37.4
18/19	200	4	1	312	34.9
19/20	40	0	0	612	15.2
20/21	55	4	2	66	12.5
21/22	25	0	0	28	5.1
22/23		1	8	0	5.6
23/24					6.2

*Partial counts.

https://doi.org/10.4039/Ent110609-6 Published online by Cambridge University Press

and from 205 to 3480 on the 6/7 July clearly indicate invasion. The two-fold increase from 2810 to 6630 on the 8/9 July, although less obvious, is also indicative of invasion. Invasions on the 4/5, 6/7, and 8/9 July would agree with the conclusion based on catches in the clearing light trap. The one discrepancy was on 12/13 July when the high catch in the clearing light trap was not matched by a marked increase in the canopy light trap.

The first males were captured in the pheromone traps on 26/27 June about 3 days before the first male pupal case was found in the study area. Pheromone traps are very sensitive in picking up the first male emergents. On many nights, the catch per pheromone trap averaged more than 30 males (Table II). When the data were plotted, a smooth curve was drawn through the nightly catches and significant increases in density were noted on 6/7, 12/13, 16/17, and 17/18 July. These sudden increases suggested moth invasions. However, pheromone-trap catches like canopy light trap catches, are difficult to interpret. For example, the high pheromone catch on the 7/8 July (Table II) could have been the result of continuous monitoring of an invasion that occurred on the 6/7 July, or the result of a new invasion on the 7/8 July. Thus, the pheromone-trap catches (Table II) are simply interpreted as confirming moth invasions on 6/7 and 12/13 July. Finally, both the pheromone traps and light traps detected an increase in moth activity on the 16/17 and 17/18 July but the radar counts indicated that only a few moths were present in the airspace so late in the season.

In summary, the ground-based radar detected large numbers of moths in the airspace over the study area on three nights (Table III) and we suspect from corroborative light trap data that the test block was invaded on those nights. Furthermore, the clearing light trap detected two additional invasions making a total of five invasion nights.

Impact of Invasion

The first female pupal cases (emerged adults) were found on 1 July and the first egg masses on 3 July. This is the expected emergence–oviposition sequence, and it was concluded that there were few, it any, invading females in the test block before 3 July.

Branch samples were collected daily and washed in boiling water to find the pattern in oviposition in the test block from 3 to 10 July, but tree, plot, and host variations were too high to single out sudden increases in numbers of egg masses that could be attributed to the invasion of egg-carrying females.

The final egg-mass counts were taken on balsam fir on all plots in late July. In plots P1–P9, mean numbers of egg masses ranged from 7.0 to 55 masses/m^2 foliage with a block mean of 27/m^2 (Table I). Densities in the test block ranged from 17 to 73 masses/m^2 foliage with a mean of 43/m^2 (Table I). The difference between these block means was not significant (p = .08) although it had been expected that plots P1–P9 with

Table III. Sensitivity of radar, light, and pheromone traps to suspected budworm moth invasions on nights of July 4/5, 6/7, 7/8, 8/9, and 12/13

		Light traps		
Date	Radar	Clearing	Canopy	Pheromone traps
4/5 July	*	Good	Good	Poor
6/7	Good	Good	Good	Good
7/8	Good	Poor	Poor	Poor
8/9	Good	Good	Good	Poor
12/13	*	Good	Poor	Good

*Radar operated for only a few hours.

higher pupal densities would have higher egg-mass densities. Sampling overwintering larvae after egg hatch showed the expected trend, i.e. a higher mean density on plots P1–P9 (38.4 larvae/m^2 foliage) than on the test block (26.7/m^2). This confirmed that the difference in egg-mass densities between the test block and surrounding forest that received one less spray treatment was sampling variation and therefore an overall mean of 33.8 egg masses/m^2 foliage was used in the analysis of invasion impact.

Even if all resident females had survived and oviposited on the test block they probably did not lay 33.8 masses/m^2 but there is no simple way to distinguish the contribution of invaders to this total. Only indirect assessments are available and three methods were used to estimate the number of eggs deposited by invading females. In each instance we have assumed that invaders did not re-emigrate and that emigration of resident females was minimal.

(1) If it is assumed that the adults observed in the airspace over the study area invaded the area, the total invasion force would be about 70,000 moths/ha (Table II) or 50,000 females. An analysis of females taken in the clearing light trap indicated that each female carried about 65 eggs (pers. comm. A. W. Thomas, Maritimes Forest Research Centre), and, assuming these females were invaders, the invading population would have laid about 250,000 egg masses. The estimated surface area of foliage in the block was 72,000 m^2/ha of which about 40%, or upper crowns (Morris 1955, table 3), would be favorably exposed to invading females. Thus, 250,000 masses laid on 28,800 m^2 of foliage suggests that invading females could have laid 8.7 masses/m^2.

(2) Budworm egg-mass surveys are conducted each year at about 1000 sprayed and unsprayed locations in New Brunswick. At 23 low-population locations, unsprayed near our study area, the mean budworm counts on balsam fir were 2.65 females/m^2 and 22.3 egg masses/m^2 (Table IV). Assuming that emigration was minimal in the low density, unsprayed plots, then the difference in egg-mass density between the test block (33.8/m^2) and unsprayed locations (22.3/m^2), both with low resident female densities suggests that invading females laid 11.5 egg masses/m^2 of foliage.

(3) In the above example the estimated eggs per female in the 23 unsprayed survey plots was 22.3 masses/2.65 females $\times$ 17 eggs per mass $=$ 143 eggs per female (Table IV). Assuming 143 to be the fecundity of resident females then the 1.26 resident females in the test block would have laid 10.6 masses. The difference between observed (33.8) and expected (10.6) masses suggests that invading females laid 23.2 masses. However, we consider this to be the least accurate measure of invasion because any estimate of eggs per female is very sensitive to minor variations in female density *when female density is low*.

Thus, our data suggest that budworm moths invaded the test block on five nights and the cumulative oviposition by invading females was about 10 masses/m^2 of foliage. An invasion impact of 10 egg masses per m^2 is certainly not numerically excessive. In the early years of budworm spraying in New Brunswick (1952–1953) mean egg-mass

Table IV. Observed female and egg-mass densities and calculated eggs per female in the test block, surrounding sprayed plots (P), and unsprayed survey points

Location	No. of plots	Female density/m^2	Egg-mass density/m^2	No. of eggs/mass	Eggs/ female
Test block	10	1.26	33.8	13	349
Surrounding sprayed plots (P)	9	2.56	33.8	13	172
Low density unsprayed plots near test block	23	2.65	22.3	17	143

densities, ranging from 20 to 30 masses/m^2, were recorded in areas sprayed with heavy doses of DDT that left few surviving residents. We believe these estimates of 20 to 30 masses/m^2 to represent maximum invasion in an expanding epidemic and that an estimate of 10 masses/m^2 would be plausible in the current epidemic in New Brunswick which was beginning to decline in 1975.

It is difficult to assign risk value to the additional 10 egg masses per m^2 of foliage laid by invading females. It would depend largely on the ''resident'' egg-mass density of the area being invaded. It could mean the difference between moderate (acceptable) and complete stripping of the current foliage of host trees. It could also mean a significant change in the dynamics of a population because the addition of 10 masses/m^2 would sharply boost the budworm population beyond the numerical response of most of its natural enemies. On the other hand, if both forest conditions and budworm populations were similar over a large area, chances are that invasion would result in little change; the affect of invasion would probably be negated by emigration.

References

Greenbank, D. O. 1957. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. II. The role of dispersal. *Can. J. Zool.* **35**: 385–403.

——— 1963. The analysis of moth survival and dispersal on the unsprayed area, pp. 87–98. *In* The dynamics of epidemic spruce budworm populations. *Mem. ent. Soc. Can.* 31.

——— 1973. The dispersal process of spruce budworm moths. *Marit. For. Res. Cent., Inf. Rep.* M-X-39. 25 pp.

Miller, C. A., J. F. Stewart, D. E. Elgee, D. D. Shaw, M. G. Morgan, E. G. Kettela, D. O. Greenbank, and G. N. Gesner. 1973. Aerial spraying against spruce budworm adults in New Brunswick. *Marit. For. Res. Cent. Inf. Rep.* M-X-38. 35 pp.

Morris, R. F. 1955. The development of sampling techniques for forest insect defoliators with particular reference to the spruce budworm. *Can. J. Zool.* **33**: 225–294.

Schaefer, G. W. 1976. Radar observations of insect flight, pp. 157–197. *In* Rainey, R. C. (Ed), Insect flight. *Symp. Roy. ent. Soc. Lond.* No. 7. Blackwell Scientific Publications.

Weatherston, J., W. Roelofs, A. Comeau, and C. J. Sanders. 1971. Studies of physiological active arthropod secretions. X. Sex pheromone of the eastern spruce budworm, *Choristoneura fumiferana* Clem. (Lepidoptera:Tortricidae). *Can. Ent.* **103**: 1741–1747.

(Received 26 September 1977)