THE DISPERSAL PROCESS OF SPRUCE BUDWORM MOTHS

by

D. O. Greenbank

Maritimes Forest Research Centre

Fredericton, N. B.

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INTRODUCTION

The spraying of spruce budworm moths for population control was tested in New Brunswick in 1972. This was a joint research project involving Forest Protection Limited and the Maritimes Forest Research Centre (Miller et al. 1973). One way of assessing the effect of a spray program against a moth population is through comparative measurement of the local flight activity before and after spray applications and flight activity within a spray versus a non-spray control area. Techniques for measuring flight activity are readily derived from an understanding of the basic flight patterns of the spruce budworm. The assessment of a spray program would not be complete, however, without consideration of the dispersal qualities of the budworm, which are such that areas of several hundred square miles of almost budworm-free forest may be severely damaged the year following invasion by moths from neighboring infestations. This report describes recently acquired knowledge of the spruce budworm dispersal process.

Dispersal is a process which leads to the displacement and redistribution of populations in space. The direction of lateral displacement of spruce budworm moths is controlled by wind. Dispersal begins with local flight activity and while the flight pattern of female budworm is adapted to expose the population to wind-directed dispersal the flight pattern of male budworm is adapted to maintain local populations.

First, the flight patterns of male and female budworm will be described and those factors identified which lead to the presence or absence of moths available for dispersal. These observations on local flight activity were made from platforms erected above the forest canopy. Secondly, the behavior of moths involved in the aerial part of the dispersal process will be described and those factors will be identified which determine the average distance travelled by dispersing moths. These observations on moths in the airspace were made from a helicopter and a twin-engine aircraft. Finally, the efficiency of the spray program against an adult budworm population will be assessed and recommendations made for future spray programs.

LOCAL MOTH ACTIVITY

Investigations on the flight patterns of male and female budworm moth have continued over the past three summers at the Acadia Forest Experimental Station, near Fredericton. Flight activity was also measured during one summer at each of four other locations, Baisley Depôt and Green River in northwestern New Brunswick, and at Dunphy spray and control plots in eastern New Brunswick (Table 1). At all locations, observations were made from platforms erected at the top of metal scaffolding which projected 10 feet above the canopies. Observations usually began in the afternoon, but on 24 days they began before 0800 h. Observations on all days continued until darkness, 2200 h, which was one hour after sunset.

The platform at Acadia was equipped with meteorological instruments to record air temperature, wind speed, wind direction, and turbulence. These instruments were located at two heights, 45 feet or the top of the canopy, and at 65 feet. The records are now being analysed along with measurements of light intensity to determine flight thresholds.

Male Flight Activity

Typically, male moths buzz around the crown periphery usually within a few inches of the branch tips. With gusts of wind greater than six mph, the moths immediately dart into the foliage and resume flight only when the wind calms. This flight behavior appears to be directed towards locating females. When within the crown, the moths move over the foliage with wings beating rapidly, a behavior pattern of sexually excited males (Sanders 1971). Male moths occasionally fly from tree to tree. These flights follow a spiral course with rapid changes in both direction and height.

Male moth activity was measured every 15 minutes from the observation platforms. At each check, 10 instantaneous estimates were made of the number of males buzzing around the top six feet of a balsam fir crown. Male moths do not fly in the early morning, 0500 to 0700 h. The number flying increases from 0700 to 1000 h with flight activity remaining relatively constant from 1000 to 1900 h. Males are most active in the evening when light intensity is decreasing and winds are relatively calm. Peak male flight activity is just prior to sunset whereas from 2100 to 2200 h flight activity decreases. Flight activity as measured in activity chambers (Edwards 1962) and catches made by traps encaging virgin females (Greenbank 1963, Sanders 1971) have shown that male moth activity continues until about midnight and then dimished rapidly to zero at dawn.

The flight patterns of male moths are adapted to maintain local populations. Buzzing males and males flying from tree to tree usually remain in the relatively still air of the frictional zone of the canopy. Dispersal out of a forest stand is dependent upon moths crossing this boundary layer, which on most evenings extends 20 to 60 feet above the canopy, and entering the free circulating air of the atmosphere above. The flight patterns of male moths are not adapted to expose them to wind-directed emigration and the occurrence of males in the airspace is considered accidental or incidental even though on some evenings large numbers of male moths may become involved in the dispersal process.

During the 1949-1957 budworm outbreak in northern New Brunswick, spectacular budworm dispersal was viewed on two evenings from the top of a 80-foot fire tower located on the height of land (Greenbank, 1954). Counts of moths being blown past the tower increased from 1800 h to darkness when further observations were impossible. Up to 100 budworm moths per minute were counted passing the tower on July 17, 1952, and 1000 moths per minute on July 21, 1953. Higher densities could be seen through binoculars above the tower. The sex ratio of moths trapped in nets at the 80-foot height showed that females predominated in these flights; 92% females in 1952 and 77% in 1953. Nevertheless, millions of males were being dispersed on these two evenings which had clear sky conditions and unusually strong surface winds gusting to 20 mph.

Mass invasions of spruce budworm moths have been associated with the passage of cold fronts and Henson (1951) has concluded that pre-frontal thunderstorms are responsible for the initiation of mass flights. Females have usually predominated in these invasions but the sex ratio has been highly variable, ranging from 68% males in one invasion (Greenbank, 1950) to 90% females in another (Personal communication, C.A. Miller). Male moth activity clearly increases with the approach of airmass and pre-frontal storm cells, activity counts increasing 1.6 and 3.3 fold on two evenings when convective storms approached one of the observation platforms. However, male moths being swept aloft by the strong updrafts associated with storm cells, and the actual exodus of males out of a forest stand has so far gone undetected. This may be due to the natural reluctance of observers to man the platforms during electrical storms.

Female Flight Activity

Female moths remain sedentary on the foliage throughout most of the day. They never buzz around the tree crowns and if disturbed by buzzing males they make a straight direct flight to another branch or another tree.

Female moths become active in the evening when light intensity is decreasing. Their flight behavior is functionally adapted to displace the population by wind. It begins with an abrupt take-off from the branch, a steep climb to varying heights depending upon the depth of the boundary layer, and terminates with wind-directed dispersal out of the stand. At the top of the boundary layer the flight orientation of moths changes markedly from almost vertical to a shallow-angled, wind-directed climb.

Female moth activity was measured every 15 minutes, with counts being made over a two-minute period of the number of females taking-off from a cluster of 10 trees, climbing steeply, and emigrating out of a stand. Of those females that take off on a typical day, that is, a day without convective storms, 2% have departed by 1800 h, 4% by 1900 h, 25% by 2000 h, and 83% by 2100 h. Peak exodus appears to be around sunset after which time the number taking-off decreases. Light intensity decreases rapidly with the approach of cumulo-nimbus clouds and, on afternoons when convective storms are in the area, exodus flights begin earlier. However, the total number of females dispersing out of a stand is not significantly greater on days with convective storms.

The effect of light intensity on female moth activity was well demonstrated at Acadia on July 10, 1972 when a partial eclipse (95%) of the sun occurred at 1735 h. Two-minute counts of the number of females taking-off and crossing the boundary layer were made every 15 minutes, and of the 183 females that took-off from the crowns of ten trees, 13% had departed by 1800 h. In contrast, the average departure of females by 1800 h was 2.5% in 1972. The daily flight curve of females was thus advanced about one hour on July 10, in association with the earlier-than-usual decrease in light intensity. Also, on July 10, female flight activity ceased one hour earlier than usual because of the depletion of the female moth population which on that day was available for dispersal (Table 2).

At Acadia, one hundred and thirty-nine moths have been trapped while crossing the boundary layer in their steep climb. All were females and these, when placed on foliage, laid an average of 53 eggs with a range from 0 to 141. The mean number of eggs laid by gravid females collected from the same stand was 110. The number of spermatophores found on dissection of the trapped females showed all had mated at least once, and a few three times (Table 3).

MOTH ACTIVITY IN THE AIRSPACE

Flights in a Bell G2 helicopter were made on nine evenings to sample budworm moths in the airspace. In order to relate aerial density to the number of exodus flights reported at the platform at Acadia, the airspace was considered a column of air extending above the observation platform. The sampling procedure was to make two-minute flights into the wind, each flight terminating at the platform, and to count the number of moths seen through a 3 x 6 foot frame within the helicopter. Helicopter flight runs were made at different altitudes up to 1500 feet. They began in the early evening and continued until 2130 h; flight regulations prohibit helicopters flying after dark.

Although each moth is seen from the helicopter only for an instant, it is readily counted and its wing movements are particularly evident, showing that dispersing moths cannot be considered inert, windswept bodies. Confusion with other species of moths has not been a problem. Of the hundreds of moths that hit the plexiglass dome, all were identified as spruce budworm. Examination of the carcasses showed that females far outnumbered males in the airspace on all nights except July 9, 1972, the only sampling night when convective storms were in the area (Table 4).

Counts of budworm moths made from a helicopter on nine evenings provide the following information on the vertical distribution and the vertical rate of exchange of moths in the airspace. Counts for July 12, 1971, an evening with clear skies, are presented as an example (Table 5). Observers on the platform report that no moths are seen in the airspace, prior to the female exodus flights. Early in the evening the moths are concentrated at low altitudes, and a profile of aerial density decreasing with altitude continues until about peak take-off time. Subsequently, the frequency of exodus flights decreases and the aerial density profile gradually reverses, with its form at any hour being dependent upon the vertical rate of exchange of those moths already airborne. Sometime between darkness and dawn, the moths begin to descend and a profile of density decreasing with altitude must be re-established. Helicopter flights at dawn, 0500 h, have shown no moths in the airspace.

Flights in the Piper Aztec aircraft were to have been made hourly throughout the night of July 12, 1972, to determine the rate at which the moths settle out of the airspace. Unfortunately, this program had to be cancelled after the first flight, 2300 h, because of the health of the pilot. The aircraft flew at 120 mph, twice the speed of the helicopter, and budworm moths seen in the landing light beam were counted on one-minute flight runs (Table 6). This profile of the vertical distribution of moths can not be interpreted by itself and it is not known whether the moths had begun to settle by 2300 h.

In the absence of convection, the upper limit to which moths will ascend, can be determined by air temperature. If a moth is cooled below the minimum flight temperature it will fold its wings and in the absence of vertical currents must begin to fall regardless of the speed of the horizontal wind. While no moths were seen at 4000 feet, 64°F. can not be considered the minimum flight temperature of the spruce budworm (Table 6). Male and female budworm have been seen flying at 48°F.

The distance that moths travel in a night can be computed from the average number of hours they remain airborne, the mean height of flight, and the mean wind speed at this height during the flight period. Peak take-off time is 2100 h. Moths are abundant in the air-space at 2300 h, whereas no moths are flying at 0500 h. The best estimate of the number of hours that moths are airborne thus ranges from about 3 to 7. Mean height of flight is estimated at about 1000 feet. Wind speeds at this height have been measured during sampling flights and have ranged from 10 to 15 mph at 2100 h, 10 to 12 mph at 2300 h, and 6 mph at 0500 h. Average wind speed is thus estimated at about 10 mph. Provided wind direction does not change during the period of flight, the lateral distance travelled by budworm moths in a night is from 30 to 70 miles.

CAUSES OF FEMALE MOTH DISPERSAL

New Brunswick studies on spruce budworm moth activity and dispersal have shown that:-

a) Virgin females do not fly and that mated females do not fly until they have laid a portion of their egg complement.

b) The flight behavior of females is adapted to displace them away from their birthplace to other oviposition sites. In contrast, the typical flight behavior of males is adapted to maintain populations at their birthplace. Dispersal of males occur accidentally or incidentally but not adaptively.

Two opposing hypotheses can be presented to explain why female budworm disperse.

1. Dispersal is a primary function of the female and occurs regardless of population size and conditions at the habitat.
2. Dispersal is a response to adversity, with population density and behavior functions being the factors which lead to the presence or absence of moths being available for dispersal.

Studies in New Brunswick have supported the second hypothesis.

Moth activity has been studied at different stands and in different years. For each of seven plot/year combinations, statistics are provided on the number of female moths seen emigrating from the crowns of 10 trees, on current defoliation, and resident female populations on these 10 trees (Table 7). Female exodus flights have been observed at all plots except at the most lightly infested stand, G5, at Green River. Here, the observation platform was manned from 0800 h to darkness, on 14 consecutive days during the 1972 adult season, but not one female moth was seen in flight, although seven females were found settled on the foliage or on the observation platform. In contrast, male moths were seen buzzing around the tree crowns on nine of the 14 days. Thus, female moth emigration appears to be a function of populations density and in support of this, it has been noted that, when flying over lightly-infested forest which is situated upwind from heavy infestations, no moths are seen in the airspace.

On four plots, counts of female moths in exodus flights were made daily throughout most of the adult season and it was then possible to estimate the proportion of the resident female population that emigrated. Apart from G5, these estimates were high, greater than 0.9, even where current defoliation was only 40% (Table 7). However, it can not yet be argued that the entire female population emigrates from stands with budworm populations above a certain level. Resident populations are undoubtedly supplemented by invading females and IF these invaders subsequently emigrate, then their exodus flights will be included in the count. Evidence will be presented later that each female actually makes only one exodus flight in adult life.

Studies in New Brunswick support the hypothesis that female moth dispersal is a response to population pressure. However, the exodus flight is not regarded as an immediate response of the adult to adversity, such as would arise from overcrowding of moths or lack of oviposition sites. Females do not engage in exploratory flights and the exodus flight occurs early in adult life. Most of those females trapped while in the exodus flight contained only one spermatophore (Table 3), and in moderately or heavily infested stands, females with one spermatophore are only one or at most two days old. Peak emergence from pupae is between 1400 and 1600 h; that evening the females are mated, they lay their first eggs the next day, and then in the evening they emigrate. It seems reasonable therefore to postulate that conditions such as lack of food or space act on the larval stages to produce female adults that are prone to migrate.

THE EFFECT OF PHOSPHAMIDON SPRAY ON BUDWORM MOTHS

Measurement of moth activity was used as one way of assessing the effect of Phosphamidon spray on a population of spruce budworm adults (Miller et al 1973). An observation platform was erected within the 8,000 acre spray block and another platform within a control block, 5.2 air miles distant. The platform was manned from July 7 to July 16, with spray being applied at 0745 h July 12, and at 2030 h July 14.

The essential results of the spray trial were as follows: The applied spray dosage had an immediate effect on the male moth population, virtually eliminating it on the first application. The 8,000 acre spray block was not invaded by male moths from surrounding unsprayed areas. Female moths showed no immediate reaction to the spray and remained sedentary on the foliage throughout the operation. The ratio of the number of exodus flights from the control block versus the spray block was used to assess mortality of female moths due to Phosphamidon spray. Estimated mortality 12, 36, and 60 hours after spray was 44, 94, and 97%.

Results from this small pilot experiment to test the efficiency of Phosphamidon spray against a spruce budworm adult population must be considered extremely encouraging. The control of spruce budworm epidemics through adult spraying would seem an attractive possibility. Future adult spray programs in New Brunswick should be designed to first reduce populations within a 30-40 mile strip along the western periphery of the New Brunswick infestation. Because of New Brunswick wind patterns, invasion of this strip by populations to the east would be insignificant. Each year the strip to be sprayed should be further to the east.

The target of an adult spray program is the female moth before she lays her first eggs and disperses out of the stand. At any locality, female moth emergence continues over about a 10-day period but some 70% of the female population usually emerges over a four-day period. To enlarge the target size on any date, the first spray application should be timed to coincide with peak male moth emergence. Male moth emergence usually begins two or three days earlier than female moth emergence and the removal of the early appearing males should result in females retaining virginity for a protracted period. Virgin females do not disperse. The second spray application should be three to four days later.

DISCUSSION

New Brunswick studies have clearly differentiated the flight behavior of male and female budworm moths and have provided the explanation for females predominating in wind dispersal. The average distance that moths are dispersed in a night has been estimated at between 30 and 70 miles, and this estimate can be refined after a few night flights in which the rate of settling of moths from the airspace is measured.

From New Brunswick studies, there is good evidence for supposing that the exodus flight of a female is a function of population density. There is circumstantial evidence for supposing that unfavorable conditions at the place of birth cause adults to be produced which are prone to migrate. Further, there is some evidence for supposing that most females make only one exodus flight in adult life and that the dispersal process is not repeated by an individual, night after night over distances up to 70 miles per night. First, the number of exodus flights from heavily infested stands approximates the number of resident females in the stand (Table 7). Secondly, no females were seen taking-off and dispersing out of the lightly-infested stand, G5, in 1972 and yet there was ample evidence that this stand was invaded on at least two nights. Catches of 1300 and 1500 females made by a light trap, located in a clearing within the stand, were out of all proportion with the resident female population available for trapping. All seven females found resting on the observation platform or on the foliage were spent. Thirdly, there is a discrepancy between the androus condition of females which emigrate out of a stand and the androus condition of females in the stand. Of 139 females trapped while in the exodus flight from Acadia only 16% had mated more than once (Table 3). In contrast, vacuum collections of females made daily from the foliage throughout an adult season showed, that of 810 mated females collected, 47% had mated more than once (Personal Communication, I. Outram). Finally, the cartographic presentation of the massive spruce budworm outbreak in eastern Canada from 1937 to 1949, shows a progressive west to east spread of the area of severe infestation from the Mississauga region in central Ontario, through Quebec, to north-west New Brunswick, a distance of 800 miles in 12 years, or 65 miles per year (Brown, 1970).

The use of helicopters and aircraft has unquestionably provided new insight into the dispersal process. However, these findings are only relevant to everyday turbulent wind dispersal and new techniques, such as radar, are now required for studying dispersal associated with convectional storms.

During the adult season, one or two convectional storms can be expected to pass over any region of New Brunswick in the afternoon or evening. The association of moth invasions with the passage of prefrontal and airmass storms is well known, and the sudden deposition of inordinate numbers of budworm moths simultaneous with heavy downpours has been documented in New Brunswick on six occasions. The sex ratio of the invaders has been determined from moth collections made around lights and these ratios have been highly variable, ranging from 32% females on one night to 90% females on another. While such collections do not necessarily provide good indication of the actual sex ratio of the dispersing population, males being more readily attracted to light than females, variable sex ratios of the populations involved in convectional transport should nevertheless be expected. A storm cell which passes over an infestation in the afternoon would absorb those females which were stimulated into earlier-than-usual exodus flight and those buzzing males which were accidentally or incidentally swept aloft by the strong updrafts. In contrast, at sunset the airspace is already full of females and the addition of those males, swept aloft with the passage of a storm in the late evening, would dilute to a lesser extent the sex ratio of the population available for convectional transport.

SUMMARY

1. Male and female budworm moths have flight patterns that are identifiably different.
2. Male moths are active throughout the day and night except 3 or 4 hours around sunrise. The typical male flight behavior, that of 'buzzing' around the crown periphery, is directed towards locating females. The male flight pattern is adapted to maintaining local populations, and emigration out of the stand is accidental or incidental and usually in association with convective storm updrafts.
3. Female moths are less active than males and remain sedentary on the foliage until evening. The female flight pattern begins with an abrupt take-off from the tree, a steep climb to heights up to 60 feet above the canopy, and terminates with wind-directed dispersal out of the stand. The flight pattern is adapted to the lateral displacement and redistribution of populations.
4. The exodus flight of females is a function of population density. Females do not emigrate out of lightly infested stands.
5. Dispersing females carry about half their original egg complement.
6. The average distance that females are dispersed in a night is estimated to be between 30 and 70 miles.
7. There is evidence to suggest that females make only one exodus flight in adult life and that the dispersal process is not repeated by an individual night after night.

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LIST OF TABLES

Table 1. Description of Flight Activity Study Plots

	Stand Type %Softwood	%Hardwood	Balsam fir Ht. ft.	Age	D.B.H. ins.
Acadia Forestry Station	90	10	45	65	5.5
Baisley Depot	95	5	45	50	5.5
Green River G5	100	0	50	53	5.8
Dunphy Control	90	10	40	40	4.6
Dunphy Spray	100	0	35	40	4.5

Table 2. The diurnal cycles of female exodus flights and light intensity for July 10, 1972, eclipse of Sun, and for the 1972 adult season at Acadia Forestry Station

	July 10, 1972		1972 Season average	
Time (Hrs)	Accumulated % departure of females	Light intensity (ft-c)	Accumulated % departure of females	Light intensity (ft-c)
1500	0	12000	0	8000
1530	0	12000	0	9800
1600	0	4300	0.5	8000
1630	0	4700	1.5	6400
1700	0	4400	2.0	4850
1730	0	40	2.5	4500
1800	13	1000	2.5	3850
1830	29	800	3.0	3000
1900	35	1250	4.0	2350
1930	66	325	15	1350
2000	79	325	29	850
2030	84	225	56.5	425
2100	100	100	85	125
2130	100	5	95	10
2200	100	0	100	0

Table 3. Egg and spermatophore complements of females dispersing out of a stand at Acadia Forestry Station

Year	No. ascending females trapped	Mean No. eggs laid	% females with -- spermatophores 1	2	3
1970	42	46	86	12	2
1971	45	54	80	16	4
1972	52	59	87	11	2

Table 4. Percentage females and spermatophore counts of spruce budworm moths collected in the free airspace on different nights

Date	No. moths collected	Per cent females	% females with -- spermatophores 1	2	3
July 13, 1971	20	90	89	11	0
July 16, 1971	12	100	50	50	0
July 4, 1972	6	100	-	-	-
July 6, 1972	15	93	86	14	0
July 10, 1972	20	85	88	12	0
July 13, 1972	8	100	-	-	-
July 9, 1972	40	60	80	12	8

Table 5. Counts of budworm moths made from a Bell G.2 helicopter on July 12, 1971

Altitude (ft)	Time (h)				
	1920–1945[a]	1957–2025	2026–2100[b]	2103–2114	2116–2125
1300		0	16		
1200					
1100		0			
1000					
900	0	0	19		36
800					
700	0	3	15	27	32
600					
500	0	2	15	20	
400	0	2	10		
300					
200	0	5	8	11	15

a. Female exodus flights began at 1940 hours.

b. Peak of female exodus flights at 2045 hours.

Table 6. Counts of budworm moths made from a Piper Aztec aircraft at 2300 hours, July 12, 1972

Altitude (ft)	Budworm moths	Air Temperature °F	Wind Speed mph
4000	0	64	
3000	3	66	
2500	13	-	
2000	20	71	10-15
1000	140	72	10-12

Table 7. Resident female populations, current defoliation, and counts of female moths emigrating from different study plots

Year	Location	Resident population Emerged female pupae/10 sq. ft.	Current defoliation %	Counts of females in exodus flight	No. of days of observations	Proportion of resident population emigrating
1970	Acadia Forestry Station	13.9	65	491	5	
1971	Acadia Forestry Station	15.2	70	849	14	1.05
1971	Baisley Depot	8.4	70	439	7	
1972	Acadia Forestry Station	12.5	90	852	14	0.98
1972	Dunphy Control	5.7	40	254	12	0.95
1972	Dunphy spray	11.7	75	235	5	
1972	Green River G5	0.15	15	0	14	0.0