



Canada
United States
Spruce Budworms
Program

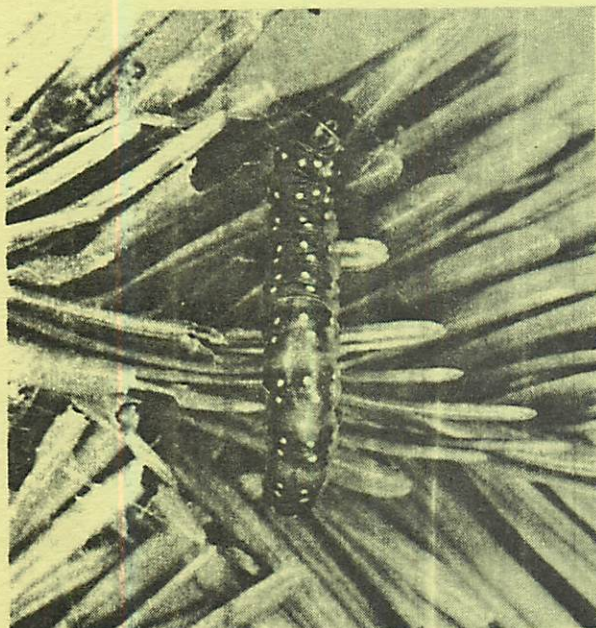
A CONTRIBUTION OF THE
NEWFOUNDLAND FOREST
RESEARCH CENTRE

N-X-181
ISBN 0704-7657

Biology and Habits of the Eastern Spruce Budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae) in Newfoundland

by

H. R. Crummey and Imre S. Otvos



Environment
Canada

Forestry
Service

Environment
Canada

Service
des Forêts

Environment
Canada

Forestry
Service

BIOLOGY AND HABITS OF THE EASTERN SPRUCE BUDWORM, CHORISTONEURA
FUMIFERANA (LEPIDOPTERA: TORTRICICAE) IN NEWFOUNDLAND

by H.R. Crumney and Imre S. Otvos

NEWFOUNDLAND FOREST RESEARCH CENTRE
ST. JOHN'S, NEWFOUNDLAND
INFORMATION REPORT N-X-181

FEBRUARY 1980

TABLE OF CONTENTS

	<u>Page</u>
ABSTRACT	i
RÉSUMÉ	ii
LIST OF TABLES	iii
LIST OF FIGURES	iv
LIST OF APPENDICES	v
INTRODUCTION	1
MATERIAL AND METHODS	2
Study Area	2
Sampling Methods	3
Determination of Larval Instars	4
Fecundity of Budworm Adults	5
RESULTS AND DISCUSSION	6
Life History	6
Eggs	6
Larvae	9
Larval Habits	12
Pre-pupae and Pupae	18
Adults	20
Fecundity of Spruce Budworm Adults	20
SUMMARY	23
ACKNOWLEDGMENTS	26
REFERENCES	27
APPENDICES	30

ABSTRACT

The eastern spruce budworm, Choristoneura fumiferana (Clemens) was not considered to be an important pest in Newfoundland until 1973, consequently, its local biology was not known. Studies recently completed show that the life cycle of this insect in insular Newfoundland is the same as throughout eastern North America, but, seasonal development occurs two or three weeks later than in the Maritime Region in Canada. The main host trees of the spruce budworm in Newfoundland are balsam fir, white spruce and black spruce. Eggs are deposited on host species from about mid-July to mid-August; eclosion occurs in about two weeks, and the insect overwinters as a second instar larva. Larval activity in Newfoundland begins at about the end of May or early June. Emerging second instar larvae mine needles or vegetative buds on all three host species. Staminate flowers are also eaten when present. Larval development is usually completed by the end of July. Pupation occurs between mid-July and early August, and moth emergence takes place after about 2 weeks.

RÉSUMÉ

Jusqu'en 1973, la tordeuse des bourgeons de l'épinette dans l'Est, Choristoneura fumiferana (Clemens) n'était pas considérée comme importante à Terre-Neuve, par conséquent on ne connaissait pas ses caractéristiques biologiques locales. Des études récentes indiquent que le cycle vital de cet insecte est le même sur l'île de Terre-Neuve que dans tout l'est de l'Amérique du Nord, mais que le développement saisonnier a lieu deux à trois semaines plus tard que dans les Régions Maritimes du Canada. A Terre-Neuve, le sapin baumier, l'épinette blanche et l'épinette noire sont les hôtes favoris de la tordeuse. La tordeuse pond ses oeufs sur ces essences à partir de la mi-juillet jusqu'à la mi-août; l'éclosion se produit deux semaines plus tard environ et l'insecte hiberne à l'état d'une larve de deuxième stade. À Terre-Neuve l'activité larvaire reprend vers la fin mai ou le début juin, et les jeunes larves attaquent les aiguilles ou les bourgeons végétatifs. Les fleurs à étamines, quand il y en a, sont aussi dévorées. Le développement larvaire est habituellement terminé vers la fin juillet. L'insecte passe au stade de chrysalide entre la mi-juillet et le début d'août et le papillon émerge environ deux semaines plus tard.

LIST OF TABLES

	<u>Page</u>
Table 1. Comparison of mean head capsule width (mm) of spruce budworm larvae from the three host tree species in Newfoundland for 1973 and 1974 (observed) with those calculated according to Dyar's theory of geometric progression (expected)	11
Table 2. Comparison of mean head capsule widths (mm) between Newfoundland and Ontario spruce budworm larvae.....	13
Table 3. Percent of larval population found in needle mines, in buds, in flower cups and crawling during feeding period of the budworm on the three host trees	15
Table 4. The average number of eggs laid by groups of females on small, caged balsam fir trees in the field	22

LIST OF FIGURES

	<u>Page</u>
Figure 1. Schematic life history of the eastern spruce budworm in Newfoundland	7
Figure 2. Average cumulative heat units ($^{\circ}\text{C}$) at Fredericton, New Brunswick and at Pasadena, Newfoundland, 1961 to 1978 inclusive	8
Figure 3. Frequency distribution of head capsule widths of spruce budworm larvae collected from balsam fir, 1973 (n = 1,267)	10
Figure 4. Average number of spruce budworm larvae and pupae by collection date based on ten 45 cm branch tips per sample date	19

LIST OF APPENDICES

	<u>Page</u>
APPENDIX A. Average number of spruce budworm (+ S.D.) per the three types of sample units based on the numbers collected from 18-inch (45.7 cm) branch samples from balsam fir by collection dates, Pasadena, 1973	30
APPENDIX B. Average number of spruce budworm per the three types of sample units based on the numbers collected from 18-inch branch samples from the three host tree species by collection dates, Pasadena, 1974	31

BIOLOGY AND HABITS OF THE SPRUCE BUDWORM,
CHORISTONEURA FUMIFERANA (LEPIDOPTERA: TORTRICIDAE)
IN NEWFOUNDLAND¹

H.R. CRUMMEY² and IMRE S. OTVOS³

INTRODUCTION

The eastern spruce budworm, Choristoneura fumiferana (Clem.), is a native insect, and is the most destructive and widely distributed defoliator of softwood forests in North America. The favored hosts in eastern North America are balsam fir, Abies balsamea (L.) Mill., white spruce, Picea glauca (Moench) Voss, red spruce, P. rubens Sarg., and black spruce, P. mariana (Mill.) B.S.P. The insect periodically causes mortality of its main host species after several years of severe defoliation (Prebble and Carolin 1967). In Newfoundland, the budworm primarily feeds on balsam fir, white spruce and black spruce, but under certain conditions it may also defoliate eastern larch, Larix laricina (Du Roi) K. Koch.

Outbreaks of the spruce budworm in North America have occurred on at least five separate occasions since the early or mid- 1700's. These outbreaks occurred at irregular intervals, lasted for several years and caused extensive tree mortality (Greenbank 1963b; Blais 1965).

¹Partly from a thesis submitted by H.R. Crummey to Memorial University, St. John's, Newfoundland, in partial fulfillment of the requirements for an M.Sc. degree.

²Department of Forest Resources and Lands, Government of Newfoundland and Labrador.

³Newfoundland Forest Research Centre, Canadian Forestry Service, Department of Environment, St. John's, Newfoundland.

These losses made the spruce budworm an economically important forest pest extensively studied throughout most of its range (Blais 1952, 1953, 1965; Morris 1963; McKnight 1968; and others).

In Newfoundland, only small, scattered outbreaks of the spruce budworm have been recorded prior to 1972 (Otvos and Moody 1978). These outbreaks have usually collapsed within a few years without causing extensive damage, and the insect was therefore not considered to be an important pest on the Island prior to that time. Consequently, it was not studied in Newfoundland until 1972 when the first widespread outbreak began.

This paper reports results of a two year study on the life history, habits, and duration of various life stages of the spruce budworm on insular Newfoundland. It also compares these results with observations made at other locations in eastern North America.

MATERIALS AND METHODS

Study Area

The study area was located near Pasadena in western Newfoundland, in a partially cutover, mixed stand of balsam fir, black spruce and some white spruce. Trees were semi-open grown, approximately 7-10 m tall and between 30-40 years old and supported a second instar larval population of 45 and 72 larvae/45 cm branch tip in 1973 and 1974 respectively. Only balsam fir was sampled in 1973 (Appendix A), and balsam fir, black spruce and white spruce were sampled in 1974 (Appendix B).

Percent defoliation of new growth was estimated ocularly on all sample trees with binoculars in both years in August after feeding was completed.

A 7-day hygrothermograph and a rain gauge were operated in the study area from late May to the end of August during the study period. Cumulative heat units (degree days) were calculated from daily maximum and minimum temperatures from 1 April to 31 July using a lower threshold of temperature 5.56°C (42°F), with the sine curve method (Baskerville and Emin 1969) in both years to determine the relationship between heat units and development of spruce budworm larvae.

A long-term average cumulative heat unit curve was calculated for Deer Lake, the nearest weather station to the study area, about 30 km away, and compared with a similar heat unit curve for Fredericton, N.B. Heat units were calculated as above and averaged over 1961-1978 inclusive. Both stations represent the warmer part of their respective geographic region.

Sampling Methods

Budworm density was estimated by counting larvae and pupae either on clipped branch tips or from samples obtained by beating the foliage on one side of the sample trees as described by Harris et al. (1972). In the former, one 45 cm branch tip was cut with a pole pruner, equipped with a basket, from the mid-crown of each of 10 sample trees and placed separately into a plastic bag and stored at 5°C until examination. The following data were recorded for each of the branch tips: (1) foliated length and foliated width of the branch at mid-length; (2) number of buds or new shoots; (3) number of mined needles; (4) number of

buds and shoots attacked; (5) number of staminate flowers; (6) number of live and dead budworm larvae in buds, shoots, needles or staminate flowers, and number of pupae; (7) percent defoliation; and (8) number of egg masses. The number of rows and total number of eggs per mass were also determined.

In 1973, balsam fir branch tips were sampled until about mid-June when larvae became open feeders on the new shoots and then beating samples were taken. Samples were collected at three or four day intervals from 10 randomly selected trees. Five sets of samples, 10 trees each, were taken using the branch method. The same 50 trees were re-sampled using the beating method. Beating samples were taken from mid-June every three or four days throughout the development period of the budworm. Both live and dead spruce budworm larvae and pupae were recorded.

In 1974, only branch tip samples were collected once a week from 10 randomly selected trees from each of the three host species. The same 30 trees were re-sampled weekly until budworm development was completed.

Determination of Larval Instars

Up to 150 larvae, collected at each sample date, were preserved in 70% ethyl alcohol for head capsule measurements. The maximum head capsule width of each larva was measured with an ocular micrometer attached to a dissecting microscope. Larvae were classified for sex by the presence or absence of visible gonads in the fourth to sixth instar stage.

Fecundity of Budworm Adults

Adults, reared from field collected pupae, were used to determine fecundity. Pupae were sexed, the sexes reared separately and emerging adults were paired. Two types of oviposition experiments were conducted: (a) with single-pair matings in the laboratory, and (b) multiple-pair matings in the field.

Individual pairs of emerging budworm were placed into 450 ml glass jars which had been lined with paper towel and covered with screen, and provided with fresh foliage placed in water. In 1974, pupae that had fed as larvae on one of the three host species were used, 18 pairs from balsam fir and 16 pairs from each of black spruce and white spruce.

Multiple-pair mating experiments were conducted in the field on individually caged trees. Trees, about 1 m high, were transplanted from a budworm free area in the spring into a nursery, and were covered with Saran insect screening prior to emergence of adults. In 1973, 10 pairs of adults were placed on each of three trees, and in 1974 five pairs of moths on each of two trees. Both years only adults emerging from pupae collected from balsam fir were used.

Both laboratory and field experiments were terminated when the adults had died. All egg masses were collected and the eggs were counted with a dissecting microscope. Empty egg shells were stained blue (Leonard et al. 1973) to facilitate counting.

RESULTS AND DISCUSSION

Life History

The life cycle of the spruce budworm in Newfoundland is the same as throughout eastern North America except for a delay of two to three weeks in seasonal development compared with most of other parts of eastern Canada (Figs. 1 and 2). This is probably due to the later spring and somewhat slower accumulation of heat units in Newfoundland.

Eggs

Egg laying began about the third week in July, reached a peak at about 1 August, and was completed by the second week of August (Fig. 1), about two weeks later than in New Brunswick (Miller 1963a). Egg masses were almost invariably found on the underside of balsam fir needles and on either the 'upper' or 'lower' sides of spruce needles. This is similar to that recorded in mainland Canada (Blais 1952; McGugan 1954).

In this study the average number of eggs per mass was 21 ($N = 34$, range: 4 - 40). McGugan (1954) reported an average of 20 eggs per mass (range: 1 - 60) and Miller (1963c) also found a similar number in New Brunswick with considerable variation.

In a later study in Newfoundland Otvos (1977) found an average of 25 eggs per mass ($N = 170$). Although there seems to be a great variability in the ranges the average number of eggs per mass is fairly consistent.

In the present study, 54% of the egg masses had two rows of eggs, 20% had two rows plus a partial third, and 26% had three rows.

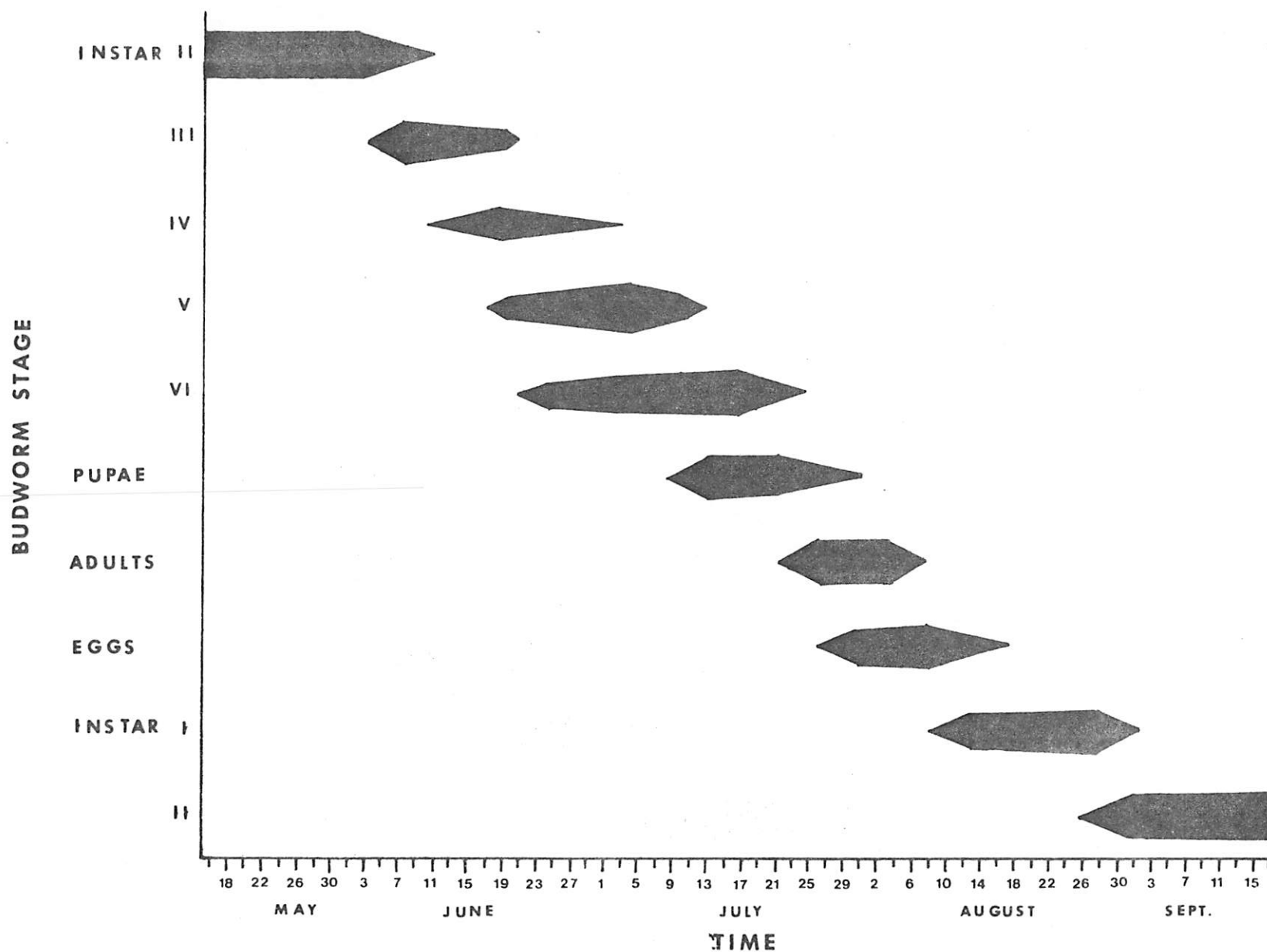


FIGURE 1.- Schematic life history of the eastern spruce budworm in Newfoundland.

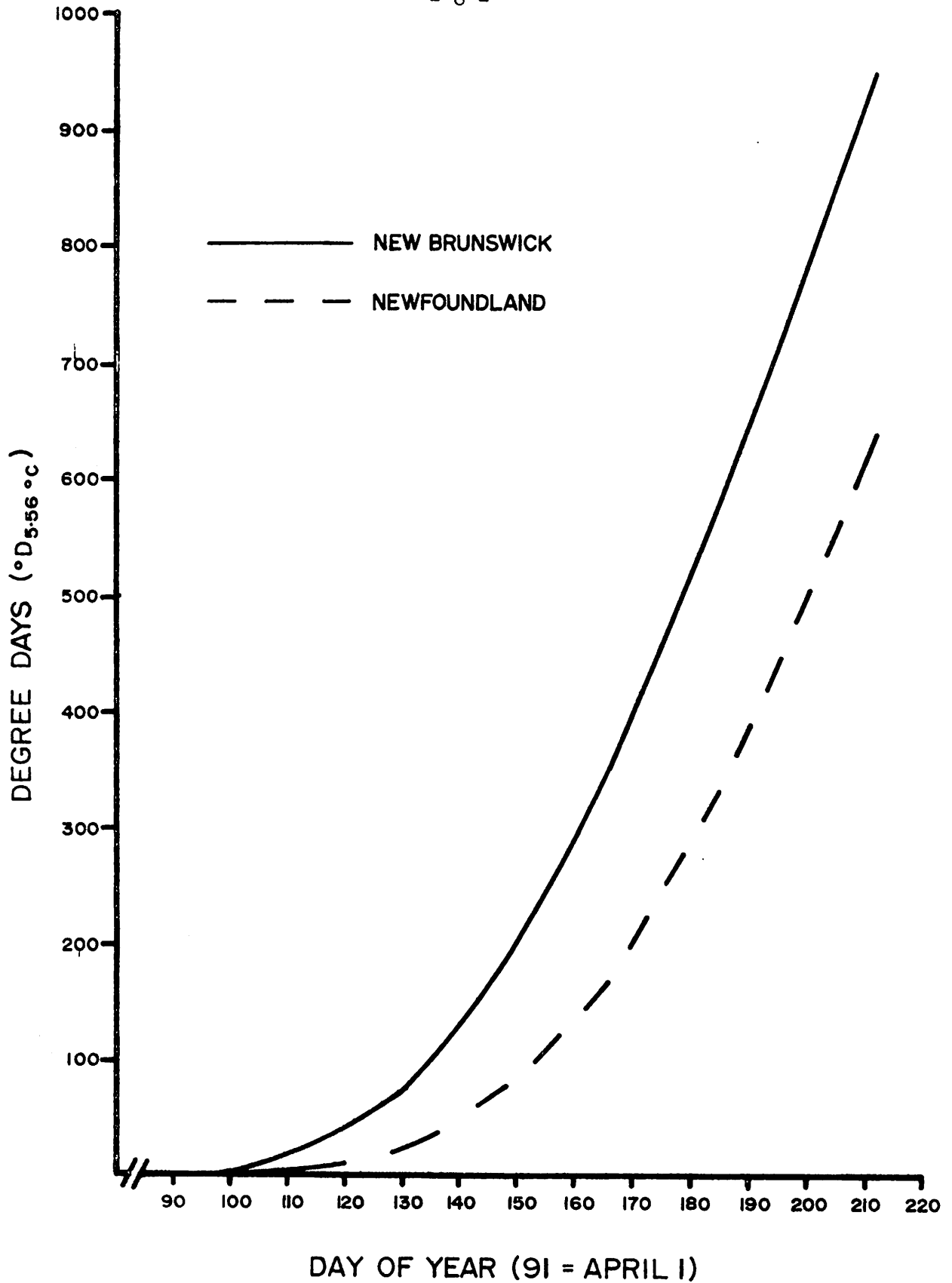


FIGURE 2. Average cumulative heat units ($^{\circ}\text{C}$) at Fredericton, New Brunswick and at Pasadena, Newfoundland, 1961 to 1978 inclusive.

Corresponding figures reported in Maine were 49%, 13% and 38% (Leonard et al. 1973). In a later study in Newfoundland, however, only 24% of the egg masses contained two rows, 67% had three rows and 9% had four rows of eggs (Otvos 1977).

Larvae

The interval between observing the first egg masses and the first instar larvae in the field was two weeks (Fig. 1) suggesting that larvae hatch in approximately two weeks under Newfoundland conditions. This is somewhat longer than the average of 10 days reported by McGugan (1954) in northwestern Ontario, and may be a reflection of climatic differences.

Head capsule widths of 1,267 and 841 larvae were measured in 1973 and 1974, respectively. A frequency distribution of these measurements in 1973 showed six major peaks (Fig. 3) suggesting this many larval instars. Observed head capsule width of larvae collected from balsam fir in 1973 and from the three host tree species in 1974, were compared to expected head capsule widths calculated according to the theory of geometric progression proposed by Dyar (1890) (Table 1). The measured (observed) values did not differ significantly from the calculated (expected) values (Table 1) from which we concluded that the spruce budworm has six larval instars in Newfoundland, as in other parts of Canada.

There was considerable overlap between instars, especially the last three. This overlap can be attributed to sex differences and the influence of parasitoids on larval development and size. Differences between sexes based on head capsule widths in the last three instars was

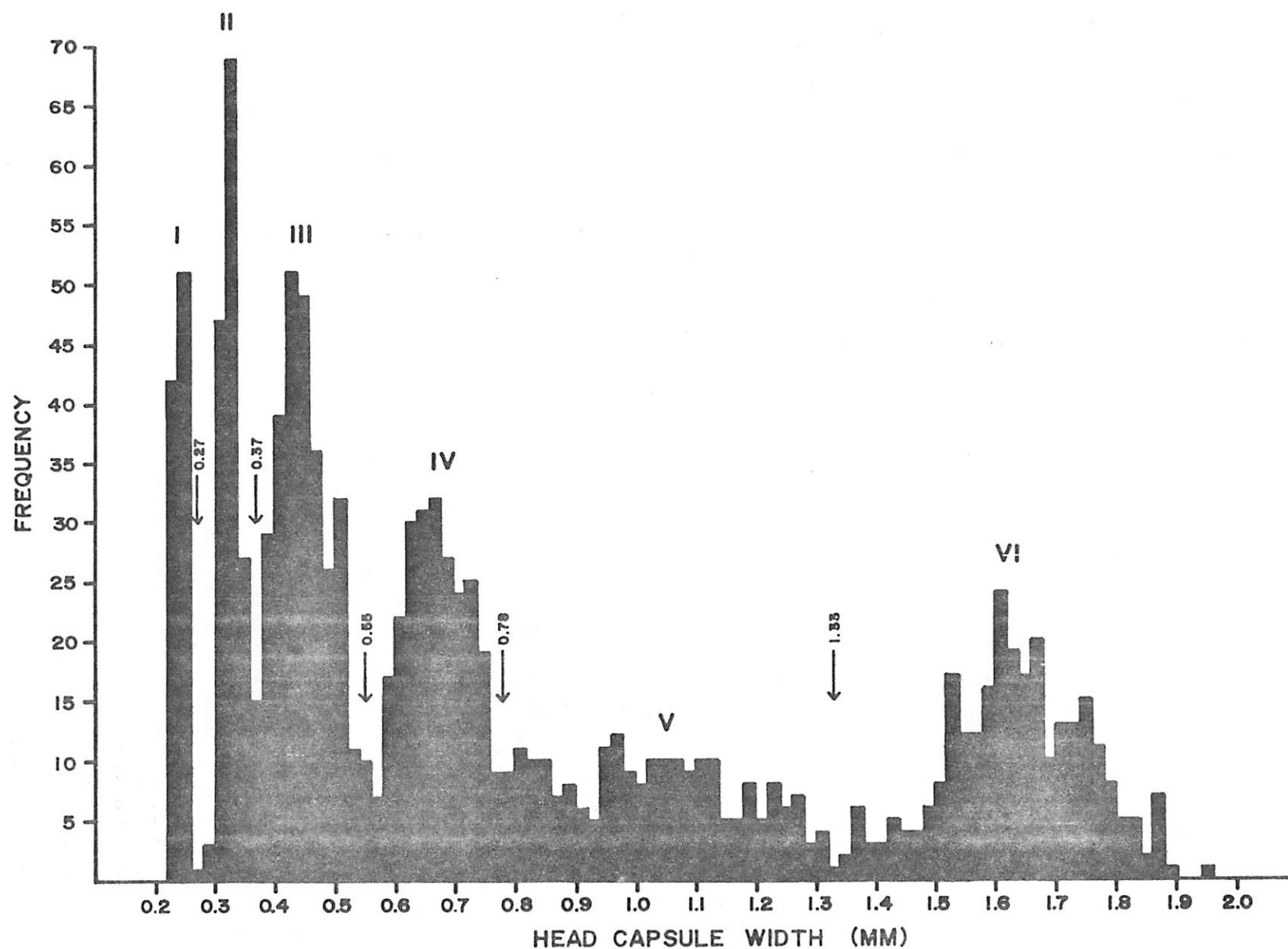


Figure 3. Frequency distribution of head capsule widths of spruce budworm larvae collected from balsam fir, 1973 (n = 1,267). Arrows indicate separation among instars.

Table 1. Comparison of mean head capsule widths (mm) of spruce budworm larvae from the three host tree species in Newfoundland for 1973 and 1974 (observed) with those calculated according to Dyar's theory of geometric progression (expected).

		1973		1974					
		Balsam fir		Balsam fir		Black spruce		White spruce	
		Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
Instar	I	0.246	0.246	0.247	0.247	*		*	
Instar	II	0.332	0.359	0.321	0.363	0.317	0.317	0.317	0.317
Instar	III	0.455	0.524	0.435	0.534	0.455	0.485	0.435	0.485
Instar	IV	0.672	0.766	0.648	0.785	0.612	0.742	0.685	0.742
Instar	V	1.028	1.118	1.050	1.153	1.097	1.135	1.017	1.135
Instar	VI	1.637	1.632	1.646	1.695	1.676	1.737	1.732	1.737

* These larvae were not measured.

noticeable (Table 2) and were statistically significant in the fifth and sixth instars ($\bar{X} = 0.979 \pm 0.155$ for males and $\bar{X} = 1.062 \pm 0.135$ mm for females, $t = 4.08$; and $\bar{X} = 1.595 \pm 0.107$ for males and $\bar{X} = 1.664 \pm 0.122$ mm for females, $t = 4.86$; for the two instars respectively, $p < 0.01$).

Larval head capsule widths measured in this study are in agreement with those presented for Ontario by McGugan (1954), including differences in head capsule widths between sexes for the fifth and sixth instar larvae.

Larval Habits

First instar larvae were not observed to feed. These larvae search for protected sites to spin hibernacula in which they molt and overwinter as second instar larvae (Atwood 1944, McGugan 1954).

In 1974, emergence of overwintering larvae was first observed on 31 May when larvae were seen hanging by threads from branches of a semi-open grown white spruce tree. The maximum temperature for this day was 12°C. Temperatures before 31 May were below 7°C. Three days later, when the maximum temperature was 22°C, larvae were observed in large numbers on all three host tree species. Emergence of larvae continued for several days. These observations are similar to those of Rose and Blais (1954) for northwestern Ontario, where abundant larval emergence occurred after temperatures approached or exceeded 15.6°C. McGugan (1954) suggested that the beginning of larval emergence might vary as much as four weeks depending upon topography and weather. In New Brunswick, emergence generally occurs in early May (Miller 1963c) - up to four weeks earlier than in Newfoundland. This trend is substantiated by a comparison between the average cumulative heat unit curve calculated

Table 2. Comparison of mean head capsule widths (mm) between Newfoundland and Ontario spruce budworm larvae.

Instar	Sex	Newfoundland ¹		Ontario ²	
		N	$\bar{X} \pm \text{S.D.}^4$	N	$\bar{X} \pm \text{S.D.}^4$
I		94	0.246 ± 0.0071	110	0.252 ± 0.0125
II		150	0.332 ± 0.0148	117	0.314 ± 0.0140
III		289	0.455 ± 0.0424	318	0.445 ± 0.0303
IV	M	110	0.674 ± 0.0504		
	F	135	0.670 ± 0.0569	348	0.682 ± 0.0652
		245	0.672 ± 0.0540		
		"t" ⁵ value 0.58 N.S.		"t" value not given	
V	M	90	0.979 ± 0.1554	150	$1.06^3 \pm 0.0794$
	F	129	1.062 ± 0.1351	154	$1.15^3 \pm 0.0940$
		"t" value 4.08*		"t" value 50.2*	
VI	M	104	1.595 ± 0.1071	348	$1.63^3 \pm 0.0820$
	F	160	1.664 ± 0.1223	232	$1.79^3 \pm 0.0897$
		"t" value 4.86*		"t" value 50.2*	
Total		1,267		1,777	

¹Larvae collected from balsam fir, 1973.

²From McGugan (1954); material for measurements was also collected from balsam fir S converted into S.D.).

³Third \bar{X} decimals not given.

⁴The standard deviation from Newfoundland was calculated to four decimal places to facilitate the comparison with the data given in McGugan (1954).

⁵Values are calculated for differences of mean head capsule width between sexes.
*90% level.

for Fredericton and Deer Lake which showed that heat units of any given level generally took two to three weeks longer to accumulate at Deer Lake than at Fredericton (Fig. 2). It should be noted that geographic location, topography and exposure, and stand characteristics such as composition and density have an effect on the seasonal development of the budworm, resulting in some variation even between adjacent areas.

Needle mining was usually the first sign of feeding activity of second instar larvae in the spring (Table 3). Entrance holes were located on the underside, near the base or middle, of balsam fir needles. The larvae first spun small shelters of silk on the surface from which they entered the needles. Holes in the needles of both spruce species were on the upper side, towards the apex. Two or three spruce needles were usually webbed together prior to mining, and these were usually all fed upon to some extent. Mined spruce needles were more easily dislodged from the branches than were mined fir needles. Mining occurred most frequently in the youngest foliage present.

Larvae emerging from the hibernacula early in the spring usually mined needles. It was not determined whether larvae that emerged later also mined needles before feeding on vegetative buds. However, between 50% and 80% of the budworm larvae mined needles in the second instar (Table 3) suggesting that needle mining is quite common. McGugan (1954) found that most budworm larvae mined only one needle on balsam fir, but two to six needles on spruce trees before feeding on the buds. Some larvae (possibly late emergers) in this study did not appear

Table 3.- Percent of larval population found in needle mines, in buds, in flower cups and crawling during feeding period of the budworm on the three host trees.

Collection date	Peak instar	Avg. no. larvae per 45 cm tip	% budworm population in			
			needles	buds	crawling	staminate flowers
Balsam fir - 1973						
29-5-73	2	16.6	56.6	42.2	1.2	-
31-5-73	2	47.5	73.5	20.4	2.7	3.4
1-6-73	2	73.8	71.6	25.3	3.0	0.1
4-6-73	2	28.6	38.1	24.8	0.4	36.7
7-6-73	3	33.7	6.5	74.5	5.6	13.4
11-6-73	3	36.1	2.2	91.7	6.1	-
25-6-73	5	41.0	0.0	74.1	25.9	-
Balsam fir - 1974						
28-5-74	2	15.7	48.9 ¹	2.1	2.1	-
7-6-74	3	72.0	60.3	36.7	3.0	-
11-6-74	3	41.2	36.6	57.3	4.4	1.7
18-6-74	4	39.5	1.0	87.6	11.4	-
25-6-74	5	23.8	0.0	37.4	62.6	-
White spruce - 1974						
3-6-74	2	16.5	50.9	36.4	12.7	-
11-6-74	3	34.7	2.3	87.6	10.1	-
13-6-74	4	60.6	1.2	93.7	4.9	0.2
25-6-74	6	43.3	0.0	85.2	14.8	-
Black spruce - 1974						
3-6-74	2	16.4	79.9	1.2	18.9	-
11-6-74	3	20.3	64.1	25.6	10.3	-
18-6-74	4	20.2	9.8	80.5	9.7	-
25-6-74	5	15.5	0.0	64.5	35.5	-

¹Difference from 100% is due to larvae still in hibernacula; they were force-emerged and counted.

to mine any needles whereas a few occasionally mined more than one fir needle when two or three needles were webbed together.

Branches with staminate flowers, particularly from balsam fir, had more larvae ($\bar{X} = 36$, $N = 6$) than those without flowers ($\bar{X} = 18$, $N = 4$). Also, larvae found on the flowers were larger and usually more advanced in development than those occurring elsewhere on the same branch or on non-flowering branches. For example, of 286 larvae collected on 4 June 1973, 105 were found in flowers and the remainder (171) elsewhere. Of the 105 larvae in the flowers, 17% were in the second, 73% in the third and 10% in the fourth instar. Of the 171 larvae elsewhere on the branch, 78% were in the second and 22% in the third instar. Higher budworm density and enhanced larval development on flowering branches have also been observed and reported by others (Bess 1946; Blais and Thorsteinson 1948). In laboratory experiments Jaynes and Speers (1949) observed that pollen-fed larvae matured three weeks earlier than those reared on foliage. Greenbank (1963a) found that the development of larvae which fed on staminate flowers in the field was three to seven days ahead of that of non-flower feeders.

When staminate flowers were not available, larvae mined vegetative buds. Complete destruction of vegetative buds often occurred before flushing could take place, particularly on balsam fir. New shoots on white spruce developed more rapidly than on fir, and in most cases elongation commenced before important damage was done to the buds by the budworm. On white spruce, larvae often webbed the caps of bud scales to the terminal needles of the new shoots. These caps provided shelter for

early instar larvae. Shoot elongation was slowest on black spruce and consequently black spruce provided less new growth for early instar larvae than the other two host species.

When new shoots became available, larvae frequently webbed two or three together to form feeding shelters. Unless disturbed, larvae usually remained on the new foliage until it was consumed. When the new foliage was consumed larvae moved either to other shoots on the same branch or other branches, or to other trees.

Where larval density was high, "backfeeding" (feeding on older foliage) occurred. Backfeeding was not observed in 1973, but in 1974 it occurred on some sample trees. Backfeeding was most severe on balsam fir where losses were about 10% of the previous year's foliage. A loss of approximately 5% occurred on white spruce, and a trace on black spruce. Average defoliation of new foliage on the sample trees in 1974 was about 95% for balsam fir, 85% for white spruce and 70% for black spruce. Percent defoliation in 1973 was similar.

Budworm larvae were also observed to feed on larch trees located beneath, or next to heavily infested primary host trees. These larvae quickly consumed the sparse needles, completely defoliating many trees. However, even completely defoliated larch trees usually refoliated by late July. Mining of needles or buds on larch was not observed.

In 1974, peak budworm larval numbers averaged 72.0 per branch tip on balsam fir, 60.6 on white spruce and much lower, 20.3 on black spruce (Table 3). Percent larval survival, up to pupation, based on peak larval population, on white spruce, balsam fir and black

spruce was 2%, 6% and 14%, respectively. The decline in larval numbers on balsam fir and white spruce was more rapid than on black spruce. The higher survival on black spruce may have resulted from the initially lower number of larvae feeding on adequate food.

Decrease in larval numbers might have resulted from increased contact between larvae (disturbance), competition, exhaustion of the food supply (starvation), differences in phenology of the host trees, or more intense predation on balsam fir and white spruce where larval density was greater (Table 3, Fig. 4), or a combination of these. Peak larval density on white spruce occurred between the second and third week in June. This may have resulted from migration of larvae from surrounding "overpopulated" balsam fir trees. Peak larval density on balsam fir occurred in early June. Larval development on black spruce was about one week behind that on both white spruce and balsam fir. Black spruce was slowest to develop phenologically in the spring whereas white spruce provided the maximum new growth, followed closely by balsam fir. Development of larvae in northwestern Ontario was slower and mortality higher for larvae reared on black spruce than for those reared on white spruce or balsam fir (Blais 1957).

Pre-pupae and Pupae

Pre-pupal stage was estimated to last an average six days under field conditions, and it was as short as three days in the laboratory. Pupation usually occurred within the larval feeding shelters.

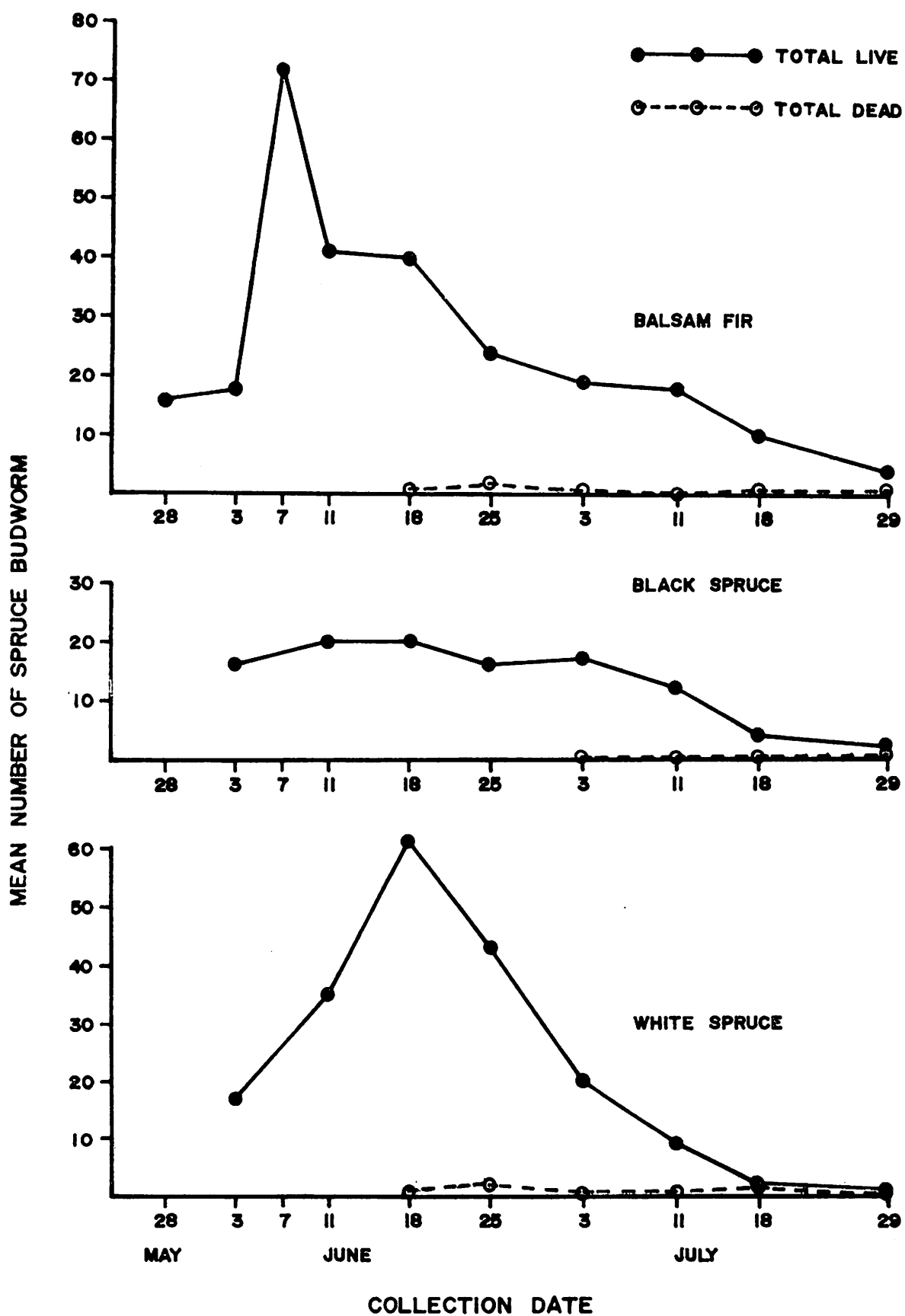


Figure 4. Average number of spruce budworm larvae and pupae by collection date based on ten 45 cm branch tips per sample date.

Duration of the pupal stage in the field at Pasadena was about 14 days compared to 8-12 days in New Brunswick (Miller 1963b). This difference is probably due to the cooler climate of Newfoundland.

Adults

Adult emergence started in mid-July at Pasadena (Fig. 1). Males emerged first, females several days later. The sex ratio of the adults was approximately 1:1, similar to that reported for New Brunswick (Miller 1963c). In the laboratory, mating occurred shortly following emergence of females, oviposition began within two or three days after emergence, and egg laying was completed within four days. Males lived for an average of only seven days without food while females lived an average of 12 days in the laboratory. The observed life span of an individual adult was approximately 14 days in the field. Flight activity of the moths in the field lasted about three weeks at Pasadena, until about mid-August. Adults were relatively inactive during the day, became active in late afternoon or early evening, and this activity continued for several hours. Moths were seen fluttering around the host trees, but not in a noticeable, active directional flight. Observations were discontinued at dusk.

Fecundity of Spruce Budworm Adults

Moth emergence from field collected pupae was relatively poor. About 67% of the pupae collected from balsam fir emerged as adults, 69% from black spruce and only 19% of the pupae collected from white spruce.

Results of egg laying by these adults, mated in individual pairs, are summarized below:

Origin of pupae	No. of females reared emerged		Total no. of eggs laid	Average no. eggs per (+ SD)	
				mass	female
Balsam fir	18	12	1023	17.2 \pm 8.0	85.3 \pm 54.7
Black spruce	16	11	1282	21.8 \pm 8.8	116.6 \pm 50.3
White spruce	16	3	98	15.9 \pm 8.0	32.7 \pm 20.5
Total	50	26	2403	19.0 \pm 8.4	92.4 \pm 55.4

The average number of eggs laid by females was 85 for balsam fir, 117 for black spruce and 33 for white spruce. These are considerably lower than the 200 eggs per female reported by Miller (1963c) and somewhat lower than the range of 100 to 200 eggs per female given by Stern (1954). The reason for the lower fecundity in the Newfoundland tests was probably caused by the amount and type of foliage consumed by the larvae in the Pasadena study and the effects of these on fecundity. Black spruce had the smallest number of larvae per 45 cm tip of the three host species and consequently sufficient new growth was present on the branches for the developing larvae in comparison with white spruce or balsam fir, where larvae were sometimes forced to feed on older needles. This may explain why survival was highest on black spruce as well as the ranking, based on the average number of eggs laid by females originating from the three host trees. Miller (1957, 1963a) showed that food quality was one

of the important factors affecting fecundity, and Blais (1952, 1953) found that fecundity decreased when larvae were fed on old foliage. Greenbank (1963a), on the other hand, reported that in the absence of food shortage fecundity was not affected by the type of host species. The unusually low number of eggs produced by females from white spruce in Newfoundland may also be an artifact introduced by the health or the few females used in the experiment or both.

The average number of eggs laid per female (mated in multiple-pairs) on small, caged balsam fir trees in the field was also less than the normally expected 200 eggs per female (Table 4).

Table 4.- The average number of eggs laid by groups of females on small, caged balsam fir trees in the field.

Year	Tree no.	No. of females/cage	Total no. of		Average no. of eggs	
			egg masses	eggs	per mass	per female
1973	1	10	29	453	15.6	45.3
	2	10	28	420	15.0	42.0
	3	10	58	981	16.0	98.1
	Total	30	115	1,854	16.1	61.8
1974	1	5	61	810	13.3	162.0
	2	5	18	295	16.4	59.0
	Total	10	79	1,105	14.0	110.5

The average number of eggs laid per female was 61.8 in 1973 and 110.5 in 1974 (Table 4). The average weight of the pupae in 1973 was about one-half of that in 1974. It is interesting to note that the average number of eggs per mass both in the individual-pair and group-mating experiment was less than the usual 20 reported from elsewhere (McGugan 1954, Miller 1963a), and also found during this study in the naturally laid egg masses in the field at Pasadena. The number of eggs laid per female both in the individual-pair and group-mating experiment was also less than the average of 200 per female reported by Miller (1963c). This lowered fecundity may have been caused by handling the pupae. Excessive handling has been reported to have a deleterious effect on survival (Miller 1963b) and it may also influence the number of eggs laid. Also, it was not determined whether females laid the entire complement of their eggs in either year.

SUMMARY

The spruce budworm is an important defoliator of the spruce-fir forests in North America, periodically causing extensive damage. In Newfoundland, budworm damage was not important until 1973, and consequently the insect had not been studied here. Studies since then showed that the life cycle of the eastern spruce budworm in Newfoundland is the same as elsewhere throughout eastern North America. However, the seasonal development of the budworm in Newfoundland was observed to be 2-3 weeks later than in most parts of eastern Canada.

Egg laying in Newfoundland began around mid-July, and was completed by about mid-August. Egg masses were usually found on the underside of balsam fir needles, while on black and white spruce they occurred on the upper or lower sides of the needles.

The presence of six larval instars were confirmed. Eclosion occurred approximately 2 weeks after egg laying and the larvae overwintered in the second instar. These emerged in late May or early June, up to 4 weeks later than reported in New Brunswick.

Needle mining is common in Newfoundland, and was observed on all three host species. Complete destruction of buds, especially on balsam fir, had also been observed before flushing of the new growth could take place. Phenological development was most advanced on white spruce followed by balsam fir and black spruce.

Backfeeding was observed on all three host species when larval population levels were high.

Branches with staminate flowers had more larvae than those without. Peak larval density on white spruce (\bar{X} = 60.6 per 45 cm branch tip) and balsam fir (\bar{X} = 72.0) was about three to four times as high as on black spruce (\bar{X} = 20.3). Decrease in larval numbers through the developmental period was more rapid on balsam fir and white spruce than on black spruce. Percent larval survival up to pupation was 6%, 2% and 14% on balsam fir, white spruce and black spruce, respectively.

Larval development was normally completed by the latter part of July. Pupation occurred from about mid-July to early August and the

pupal stage lasted about 14 days, somewhat longer than in New Brunswick.

Spruce budworm moths, emerged from pupae collected in the field, on the average, laid 92 eggs per female in the laboratory, and 74 eggs on caged trees in the field.

ACKNOWLEDGMENTS

We wish to thank our colleagues at the Newfoundland Forest Research Centre, St. John's, Newfoundland for reading the manuscript, and Mrs. D.J. Didham who typed the manuscript. We would also like to thank Dr. J.R. Blais, Laurentian Forest Research Centre, Ste. Foy, Quebec, and Mr. C.A. Miller, Maritimes Forest Research Centre, Fredericton, New Brunswick of the Canadian Forestry Service, Department of Environment, and Mr. N.E. Carter, Department of Forest Resources and Lands, Government of Newfoundland and Labrador for their review and helpful comments. The long term weather data from Fredericton was kindly provided by C.A. Miller.

REFERENCES

- Atwood, C.E. 1944. The feeding habits of the young spruce budworm larvae.
Can. Entomol. 76:64-66.
- Baskerville, G.L. and P. Emin. 1969. Rapid estimation of heat accumulation
from maximum and minimum temperatures. Ecology 50:514-517.
- Bess, H.A. 1946. Staminate flowers and spruce budworm abundance. Can.
Dep. Agric. For. Insect Invest. Bi-Mon. Progr. Rep. 2(2):3-4.
- Blais, J.R. 1952. The relationship of the spruce budworm (Choristoneura
fumiferana (Clem.)) to the flowering condition of balsam fir
(Abies balsamea (L.) Mill.). Can. J. Zool. 30:1-29.
- Blais, J.R. 1953. Effects of the destruction of the current year's
foliage of balsam fir on the fecundity and habits of flight
of the spruce budworm. Can. Entomol. 85:446-448.
- Blais, J.R. 1957. Some relationships of the spruce budworm, Choristoneura
fumiferana (Clem.), to black spruce, Picea mariana (Moench.) Voss.
For. Chron. 33:364-372.
- Blais, J.R. 1965. Spruce budworm outbreaks in the past three centuries
in the Laurentide Park, Quebec. For. Sci. 11:130-138.
- Blais, J.R. and A.J. Thorsteinson. 1948. The spruce budworm in relation
to flowering conditions of the host tree. Can. Dep. Agric. For.
Insect Invest. Bi-Mon. Progr. Rep. 4(5):1.
- Dyar, H.G. 1890. The number of molts of lepidopterous larvae. Psyche
5:420-422.

- Greenbank, D.O. 1963a. Staminate flowers and the spruce budworm. In: R.F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 202-218.
- Greenbank, D.O. 1963b. The development of the outbreak. In: R.F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 19-23.
- Harris, J.W.E., D.G. Collis and K.M. Magar. 1972. Evaluation of the tree-beating method for sampling defoliating forest insects. Can. Entomol. 104:723-729.
- Jaynes, H.A. and C.F. Speers. 1949. Biological and ecological studies of the spruce budworm. J. Econ. Entomol. 42:221-225.
- Leonard, D.E., G.A. Simmons and G.K. VanDerwerker. 1973. Spruce budworm: techniques to improve counting of eggs. J. Econ. Entomol. 66:992.
- McGugan, B.M. 1954. Needle mining habits and larval instars of the spruce budworm. Can. Entomol. 86:439-454.
- McKnight, M.E. 1968. A literature review of the spruce budworm, western, and two-year-cycle budworms, Choristoneura fumiferana, C. occidentalis, and C. biennis. U.S.D.A. For. Serv. Res. Pap. RM-44. 35 pp.
- Miller, C.A. 1957. A technique for estimating the fecundity of natural populations of the spruce budworm. Can. J. Zool. 35:1-13.
- Miller, C.A. 1963a. The analysis of the fecundity proportion in the unsprayed area. In: R.F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 75-87.
- Miller, C.A. 1963b. The analysis of pupal survival in the unsprayed area. In: R.F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 63-70.

- Miller, C.A. 1963c. The spruce budworm. In: R.F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 12-19.
- Morris, R.D. (ed.). 1963. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. 332 pp.
- Otvos, I.S. 1977. Estimating the number of eggs in spruce budworm egg masses in Newfoundland. Bi-monthly Res. Notes 33(3):17.
- Otvos, I.S. and B.H. Moody. 1978. The spruce budworm in Newfoundland: history, status and control. Environment Canada, For. Serv., Nfld. For. Res. Centre, Inf. Rpt. N-X-150, 76 p.
- Prebble, M.L. and V.M. Carolin. 1967. Spruce budworm, Choristoneura fumiferana (Clem.). In: A.G. Davidson and R.M. Prentice, ed., Important forest insects and diseases of mutual concern to Canada, the United States and Mexico. Dept. For. Rural Dev., Ottawa. pp. 75-80.
- Rose, A.H. and J.R. Blais. 1954. A relation between April and May temperatures and spruce budworm larval emergence. Can. Entomol. 86:174-177.
- Stehr, G. 1954. A laboratory method for rearing the spruce budworm Choristoneura fumiferana (Clem.) (Lepidoptera: Tortricidae). Can. Entomol. 86:423-428.

APPENDIX A

AVERAGE NUMBER OF SPRUCE BUDWORM (\pm S.D.) PER THE THREE TYPES OF SAMPLE UNITS BASED ON THE NUMBERS COLLECTED FROM 18-INCH (45.7 cm) BRANCH SAMPLES FROM BALSAM FIR BY COLLECTION DATES, PASADENA, 1973

Sample dates		Live larvae			Dead larvae		Live pupae		Dead pupae		Empty pupal cases		Live total		Dead total		Grand total	
		18" tip ^a	10 sq. ft. ^b	Feeding site ^c	18"	10 sq. ft.	18"	10 sq. ft.	18"	10 sq. ft.	18"	10 sq. ft.	18"	10 sq. ft.	18"	10 sq. ft.	18"	10 sq. ft.
May 31	\bar{X}	47.50	508.50	1.74	5.80	56.30							47.50	508.50	5.80	56.30	53.30	564.80
	S.D.	26.03	317.31	3.75	7.21	79.02							26.03	317.31	7.21	79.02	25.97	313.99
June 4	\bar{X}	28.60	432.40	0.40	0.80	11.20							28.60	432.40	0.80	11.20	29.40	443.60
	S.D.	16.96	306.20	0.57	1.23	15.88							16.96	306.20	1.23	15.88	17.46	309.58
June 7	\bar{X}	33.70	365.50	0.50	2.80	28.00							33.70	365.50	2.80	28.00	36.50	393.50
	S.D.	21.69	205.53	0.27	2.25	24.55							21.69	205.53	2.25	24.55	21.36	198.60
June 11	\bar{X}	36.10	628.10	0.54	8.80	141.00							36.10	628.10	8.80	141.00	44.90	769.10
	S.D.	13.98	553.22	0.27	3.88	109.27							13.98	553.22	3.88	109.27	15.99	656.24
June 25	\bar{X}	41.00	547.10	0.58	3.50	43.10							41.00	547.10	3.50	43.10	44.50	590.20
	S.D.	24.16	592.66	0.24	2.88	46.66							24.16	592.66	2.88	46.66	25.95	636.37
July 5	\bar{X}	11.00	134.80	0.13	3.10	38.10	1.20	14.40	0.30	3.90			12.20	149.20	3.40	42.00	15.60	191.20
	S.D.	10.21	126.60	0.10	2.60	39.97	1.40	19.77	0.48	6.35			10.15	127.60	3.03	45.57	11.53	152.36

^aN = 10 tips. ^bConverted from actual foliage area of the ten, 18-inch branches. ^cBased on the actual number of feeding sites (buds + shoots + staminate flowers) found on the ten, 18-inch branches.

APPENDIX B

AVERAGE NUMBER OF SPRUCE BUDWORM PER THE THREE TYPES OF SAMPLE UNITS BASED ON THE NUMBERS COLLECTED FROM 18-INCH BRANCH
SAMPLES FROM THE THREE HOST TREE SPECIES BY COLLECTION DATES, PASADENA, 1974

Collection date		Live larvae			Dead larvae			Live pupae		Dead pupae		Empty pupal cases		Total live		Total dead		Grand total	
		18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.
BALSAM FIR ^a																			
May 28	\bar{X}	15.67	154.67	0.230										15.67	154.67			15.67	154.67
	S.D.	2.89	31.90	0.020										2.89	31.90			2.89	31.90
June 3	\bar{X}	18.00	301.70	0.337										18.00	301.70			18.00	301.70
	S.D.	11.77	261.23	0.254										11.77	261.23			11.77	261.23
June 7	\bar{X}	72.00	777.60	1.217										72.00	777.60			72.00	777.60
	S.D.	46.46	551.78	1.638										46.46	551.78			46.46	551.78
June 11	\bar{X}	41.20	521.80	0.697										41.20	521.80			41.20	521.80
	S.D.	21.22	253.57	0.412										21.22	253.57			21.22	253.57
June 18	\bar{X}	39.50	497.00	0.687	1.00	16.50	0.012							39.50	497.00	1.00	16.50	40.50	513.50
	S.D.	16.52	303.63	0.403	0.81	21.11	0.010							16.52	303.63	0.81	21.11	16.68	322.30
June 25	\bar{X}	23.80	228.70	0.375	1.90	18.90	0.023							23.80	228.70	1.90	18.90	25.70	247.60
	S.D.	16.30	150.39	0.154	1.97	17.01	0.020							16.30	150.39	1.97	17.01	18.01	165.58
July 3	\bar{X}	19.30	326.30	0.327	0.90	19.50	0.012							19.30	326.30	0.90	19.50	20.20	345.80
	S.D.	14.13	305.28	0.175	0.88	25.17	0.010							14.13	305.28	0.88	25.17	14.17	329.34
July 11	\bar{X}	17.60	180.80	0.584	0.30	3.40	0.010	0.10	0.80					17.70	181.60	0.30	3.40	18.00	185.00
	S.D.	20.24	174.43	0.981	0.48	5.99	0.010	0.32	2.53					20.24	174.26	0.48	5.99	20.56	178.62
July 18	\bar{X}	2.40	24.70	0.041	0.50	4.30	0.010	7.60	84.70	0.10	0.90	0.10	0.80	10.10	110.20	0.60	5.20	10.70	115.40
	S.D.	1.90	17.56	0.031	0.71	5.77	0.020	10.61	126.83	0.32	2.85	0.32	2.53	12.06	139.07	0.84	7.13	12.19	141.57
July 29	\bar{X}				0.60	8.00	0.020	1.90	31.1	0.30	5.40	1.90	38.00	3.80	69.10	0.90	13.40	4.70	82.50
	S.D.				1.26	14.02	0.040	2.42	39.62	0.48	9.99	2.60	59.69	3.43	71.06	1.20	14.15	3.40	75.25

APPENDIX B (CONTINUED)

Collection date		Live larvae			Dead larvae			Live pupae		Dead pupae		Empty pupal cases		Total live		Total dead		Grand total	
		18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.
BLACK SPRUCE ^b																			
June 3	\bar{X}	16.40	212.30	0.140	0.10	0.80	0.001							16.40	212.30	0.10	0.80	16.50	213.10
	S.D.	9.64	300.08	0.084	0.32	2.53	0.003							9.64	300.08	0.32	2.53	9.85	300.27
June 11	\bar{X}	20.30	172.00	0.171										20.30	172.00			20.30	172.00
	S.D.	6.63	66.98	0.119										6.63	66.98			6.63	66.98
June 18	\bar{X}	20.20	232.60	0.304										20.20	232.60			20.20	232.60
	S.D.	9.07	125.90	0.077										9.07	125.90			9.07	125.90
June 25	\bar{X}	15.50	130.50	0.095										15.50	130.50			15.50	130.50
	S.D.	9.19	92.63	0.049										9.19	92.63			9.19	92.63
July 3	\bar{X}	17.00	156.29	0.150	0.43	3.57	0.003							17.00	156.29	0.43	3.57	17.43	159.86
	S.D.	15.56	132.27	0.107	0.53	4.54	0.005							15.56	132.27	0.53	4.54	15.54	132.29
July 11	\bar{X}	10.88	93.88	0.083	0.38	3.38	0.003	0.75	6.00					11.63	99.88	0.38	3.38	12.00	103.25
	S.D.	4.85	42.41	0.036	0.52	4.78	0.005	0.89	7.43					5.07	44.69	0.52	4.78	4.78	42.51
July 18	\bar{X}	1.30	13.00	0.025	0.20	1.60	0.001	2.80	27.60	0.10	1.30			4.10	40.60	0.30	2.90	4.40	43.50
	S.D.	1.64	20.58	0.062	0.42	3.41	0.003	1.62	17.08	0.32	4.11			2.81	33.42	0.48	4.89	2.99	36.58
July 29	\bar{X}	0.20	2.20	0.004	0.40	3.00	0.004	1.60	16.20	0.60	5.40	0.60	6.80	2.40	25.20	1.00	8.40	3.40	33.60
	S.D.	0.45	4.92	0.009	0.89	6.71	0.009	1.14	14.02	0.89	7.47	0.55	6.22	1.52	19.68	1.00	7.77	1.52	19.27

APPENDIX B (Concluded)

Collection date		Live larvae			Dead larvae			Live pupae		Dead pupae		Empty pupal cases		Total live		Total dead		Grand Total	
		18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.
WHITE SPRUCE ^c																			
June 3	\bar{X}	16.50	156.60	0.102										16.50	156.60			16.50	156.60
	S.D.	13.37	94.66	0.067										13.37	94.66			13.37	94.66
June 11	\bar{X}	34.70	365.40	0.270										34.70	365.40			34.70	365.40
	S.D.	21.42	148.41	0.122										21.42	148.41			21.42	148.41
June 18	\bar{X}	60.60	579.00	0.502	0.60	5.70	0.004							60.60	579.00	0.60	5.70	61.20	584.70
	S.D.	34.37	372.80	0.103	1.07	11.53	0.007							34.37	372.80	1.07	11.53	34.81	376.90
June 25	\bar{X}	43.30	503.60	0.485	2.20	21.80	0.019							43.30	503.60	2.20	21.80	45.50	525.40
	S.D.	14.43	341.86	0.263	3.01	30.66	0.029							14.43	341.86	3.01	30.66	16.36	341.73
July 3	\bar{X}	19.70	238.10	0.294	0.60	7.00	0.006	0.30	2.20					20.00	240.30	0.60	7.00	20.60	247.30
	S.D.	12.61	220.18	0.191	0.70	9.31	0.007	0.67	4.73					12.94	219.94	0.70	9.31	13.38	226.02
July 11	\bar{X}	8.38	103.63	0.195	1.00	7.25	0.049	0.63	5.25					9.00	108.88	1.00	7.25	10.00	116.13
	S.D.	3.89	93.22	0.200	1.51	11.65	0.045	1.06	9.42					4.60	93.46	1.51	11.65	5.07	91.54
July 18	\bar{X}	0.20	2.00	0.004	0.90	11.20	0.012	1.20	16.30	0.90	12.20	0.30	3.40	1.70	21.70	1.80	23.40	3.50	45.10
	S.D.	0.42	4.24	0.008	0.99	12.15	0.012	1.32	17.96	0.74	10.10	0.95	10.75	2.26	26.58	1.14	15.03	2.73	34.57
July 29	\bar{X}				0.20	1.60	0.010	0.30	3.40	0.20	2.40	0.60	5.80	0.90	9.20	0.40	4.00	1.30	13.20
	S.D.				0.42	3.41	0.025	0.67	8.58	0.42	5.25	1.58	14.88	1.60	15.85	0.70	6.98	2.16	20.42

^aN = 10 branch tips per sample dates. ^bN = 10 branch tips per sample dates, except on 18-6-74 (N = 5); 25-6-74 (N = 2); 3-7-74 (N = 7); 11-7-74 (N = 8); 29-7-74 (N = 5); no samples were taken on 28-5-74 and on 7-6-74. ^cN = 10 branch tips per sample dates, except on 11-7-74 (N = 8); no samples were taken on 28-5-74 and 7-6-74.