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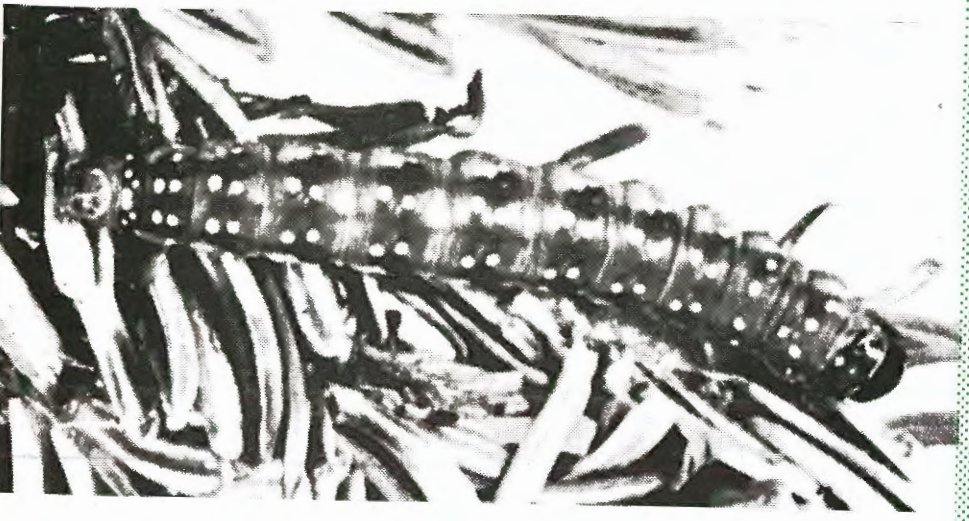

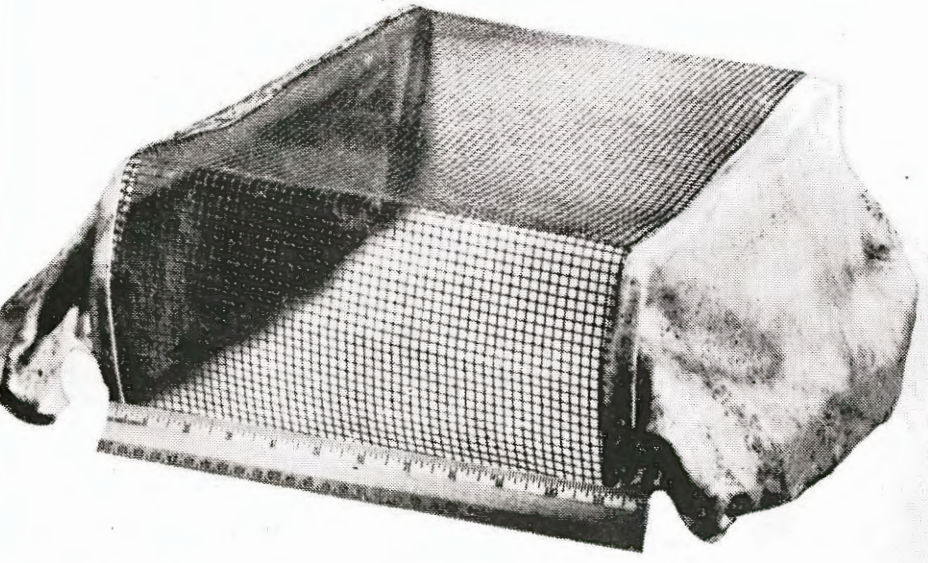

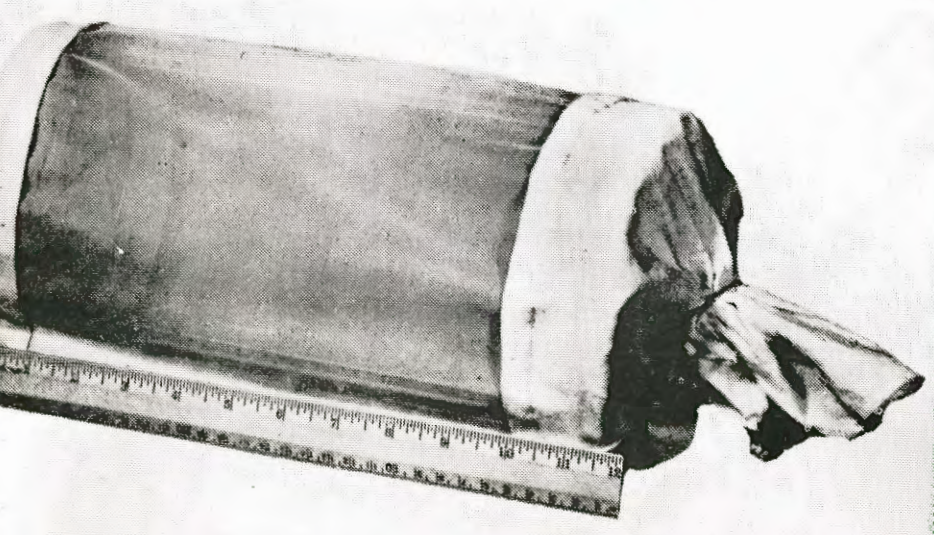

THE USE OF EXPERIMENTAL POPULATIONS TO ASSESS BUDWORM LARVAL MORTALITY AT LOW DENSITIES

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MARITIMES FOREST RESEARCH CENTRE

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ABSTRACT

Second-instar spruce budworm larvae were placed on small trees in the field and treated in three ways: enclosed in a fine-mesh cage, or a large-mesh cage, or left exposed. The objective was, through isolation, to assess some of the major mortality factors affecting a sparse budworm population. Highest mortality occurred in among late-instar larvae and pupae. Major mortality factors or processes were not identified because large larvae were unaccountably lost in the large-mesh cages.

RESUME

Des larves de la Tordeuse des bourgeons de l'Epinette du second stade furent placées sur de petits arbres sur le terrain et traitées de trois façons: encloses dans une cage de fin grillage, encloses dans une cage à gros grillage et laissés exposées. Le but de l'expérience était d'évaluer, au moyen de l'isolation, certains des principaux facteurs de mortalité affectant une population éparse de la Tordeuse. Le plus fort taux de mortalité s'est produit chez les larves et pupes de dernier stade. Il fut impossible d'identifier les principaux facteurs de mortalité, car les grosses larves furent perdues en nombre incalculable dans les cages à gros grillage.

INTRODUCTION

Sampling costs are so high that it is virtually impossible to use a 'life-table approach' to study the dynamics of an endemic population of the spruce budworm, Choristoneura fumiferana Clem. Other techniques are required. This report describes an attempt to cage budworm larvae on small trees in the field and assess the effects of disease, parasitism, and predation during the age interval, third-instar larvae (L3) to adult. The exclusion technique (sleeve cages, insecticides, biological control agents such as ants) is a common method of assessing the efficacy of certain mortality factors. Dowden et al. (1953) caged some small trees (3 to 4 m in height) with cloth and wire and left some exposed; they then checked budworm survival in each treatment. They concluded that 20 to 40% more larvae disappeared from exposed trees than from trees protected with wire screening and that birds are important predators of the budworm.

Our objective was to obtain larval mortality data that would help to explain year-to-year changes in L3 densities that were recorded simultaneously on several permanent plots in the study area. The L3 to adult age interval was selected for detailed observation because life-table data clearly show that survival of large larvae determines within-generation survival at moderate to high budworm densities, and it was assumed that this might also hold true at endemic densities.

METHODS

The study area in northwestern New Brunswick was a stand of young balsam fir that developed from a clear-cutting operation in 1947. In 1959, the average initial year of the study, the height of the codominant trees was 7.6 m. Stand density was 4500 fir and 500 white spruce per hectare. Average fir diameter was 5.6 cm. Numerous hauling roads in the area left many exposed trees with basal crown branches close to the ground. The 'resident' third-instar density in the area was assessed in three of the five study years. The sample unit was one mid-crown branch per tree and sample size ranged from 500 to 700 branches.

Year	Branches with no larvae (%)	Estimated L3 density per branch
1961	94.2	0.076
1962	97.6	0.026
1963	97.9	0.021

The data show a very low resident density. The clumped distribution of larvae is also of interest. For example, in 1961 although 94.2% of the 500 branches had no larvae, one had 5.0 larvae.

Each year a stock of budworms was obtained by forcing first-instar larvae to spin hibernacula on balsam twigs covered with old staminate flower cups. These twigs were taken to the field and pinned to the branches of young balsam fir in late August and early September in order to overwinter the stock under natural conditions. Approximately 2,000 second-instar larvae were overwintered in this manner. In early May of the following year, samples of these twigs were brought into the laboratory and checked every two days until it became apparent that emergence from hibernacula was imminent. All twigs were then collected, placed in vials, and housed in an open insectary. As the second-instar larvae emerged they were taken to the study plot and placed on the branch tips of young balsam fir at a stocking density of one larva per tree.

The second-instar larvae were placed on branch tips about 1 m from the ground and the branch tips were covered with a perforated plastic bag. This minimized dispersal from the branches before the larvae started to mine needles or buds. The bags were removed within 3 days, depending on weather conditions. About 500 second-instar larvae were established on the study plot each year on trees where cutting-trails (from previous pulpwood operations) permitted the use of relatively exposed branches with vigorous growth near ground level. The 500 larvae were therefore scattered over an area of about 1.0 ha.

In general, the second instar larvae molted to the third-instar in late May- early June and established feeding sites in the expanding current shoots. At that time they were divided into three experimental populations as follows:

Series 1 This experiment consisted of about 100 larvae each enclosed with a cylindrical cage about 30 cm long, 13 cm in diameter, and constructed of fine-mesh plastic screening (Fig. 1A). Strips of cotton cloth about 15 cm wide were used to close the ends of the cage, and a coil of wire was inserted to support and shape the plastic screening. It was assumed that the cage would exclude parasites and invertebrate and vertebrate predators, and that disease, inherent population 'vigor', and weather would be the principal sources of mortality.

Series 1A This experiment was similar to Series 1 except that the cage was somewhat larger and constructed of fine-mesh nylon (Fig. 1C) rather than plastic screening. Series 1A was used to check the potential variation in budworm survival resulting from the characteristics of the cage.

Series 2 This experiment consisted of about 100 larvae each enclosed in a box cage, 30 cm x 30 cm x 18 cm deep, made of galvanized screen of 0.6 cm mesh size (Fig. 1B). Strips of cloth were used to enclose the ends of the cage. It was assumed that parasites and invertebrate predators would have access to the caged larvae while birds would be excluded, and that this experiment would consequently provide an index of budworm survival in the absence of predation by birds.

Series 3 This experiment consisted of about 200 larvae that were left exposed until the survivors reached the adult stage.

In any one year, the series of populations were intermixed so that, for example, the exposed larvae of Series 3 were not clumped together in one part of the study area. The larvae were examined every 3 days with a minimum disturbance of the feeding site, and movement to new feeding sites was noted on a diagram of the branch. At each examination the larvae were recorded as living, parasitized, dead, or missing. Parasitized and dead larvae were taken to the laboratory. Parasites were reared to the adult stage for identification.

We had difficulty in determining the cause of death of cadavers found on the foliage. The probable causes were:

1. Disease. Flaccid, discolored larvae. Some of these larvae were frozen and examined at a later date for pathogens.

2. Inherent mortality. Many laboratory rearings of field-collected budworm larvae consistently show that some die with no diagnostic evidence of disease or parasitism. This is usually classified as 'inherent' or 'unknown' mortality (Neilson 1963).

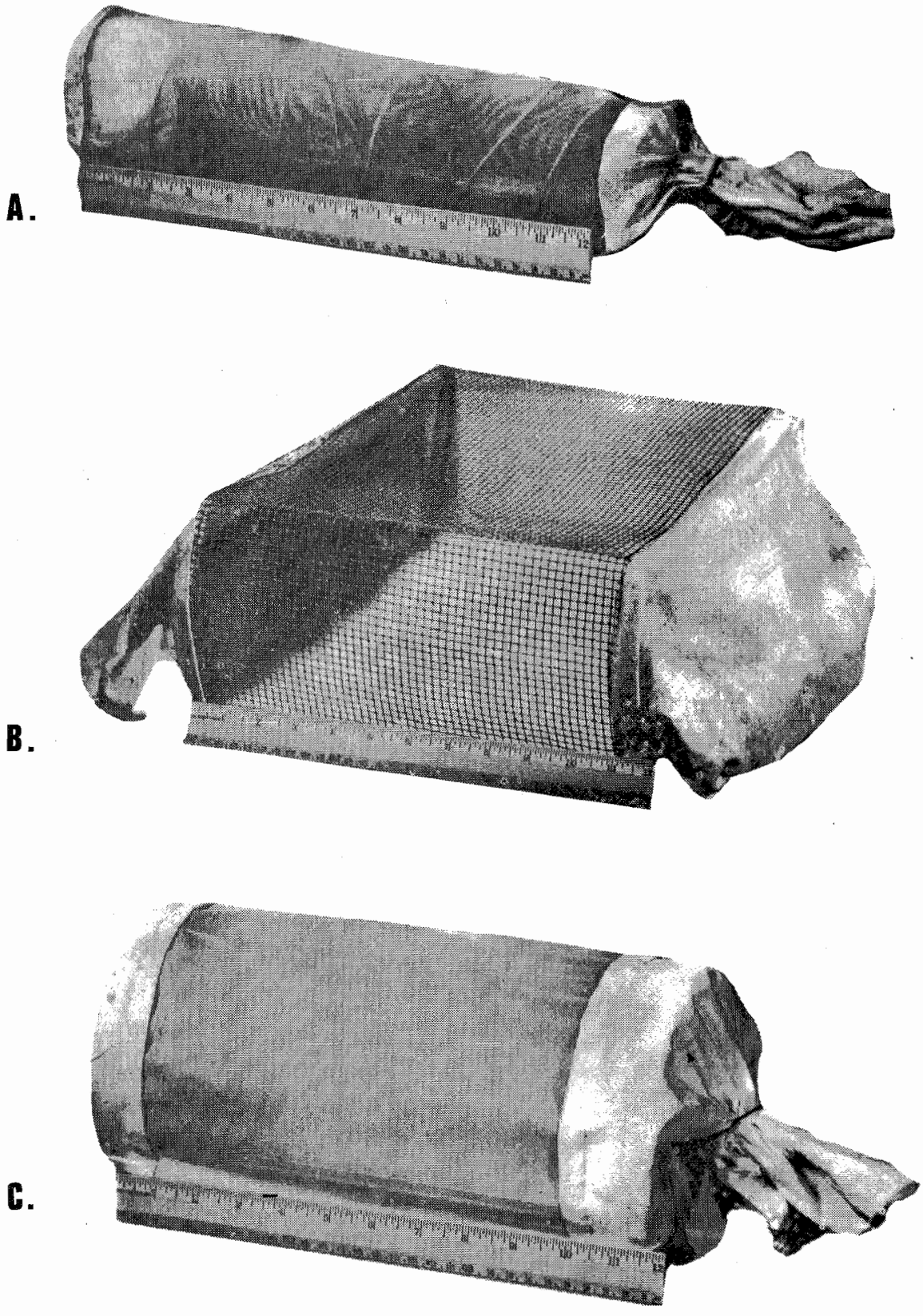

Fig. 1. Cages used in field experiments to assess budworm larval mortality at low populations.

3. Predation. We classified dead larvae with a broken integument or body contents removed as predation by small invertebrate predators.

4. Scavengers. It is likely that some larvae were killed by disease and later fed upon by scavengers. We could not distinguish these victims.

Mortality was recorded as the actual number of budworm killed by a particular factor on a particular date. This differs from the usual assessment of mortality where, for example, a sample of the host population is collected and dissected for parasites and the number of hosts with parasites is, in effect, the apparent number that would be killed by parasites in the absence of all other mortality factors. The assessment of mortality in terms of 'actual' proportions made mortality data additive in the analysis.

The analysis of the data was based on the survival rates from peak third-instar larvae (L3) to the adult stage in each series of experiments and these were further divided into survival rates from peak L3 to peak L5, peak L5 to peak L6, and peak L6 to the adult stage. To define these age intervals, budworm development was recorded at three stages each year; - peak third-instar, appearance of the first sixth-instar larva and appearance of the first pupa. In general, the first sixth-instar larva is found when the bulk of a population is at the peak of the fifth-instar, and the first pupa when the bulk of a population is at the peak of the six instar.

Development dates during the study period were as follows:

Year	First L6	First pupa	L6 age interval (days)
1959	20 June	2 July	12
1960	12 June	25 June	13
1961	28 June	8 July	10
1962	26 June	5 July	10
1963	24 June	2 July	8

The earliest development occurred in 1960. The deviation in development days relative to 1960 was as follows:

Year	Ranked deviation in days later than 1960	
	First L6	First pupa
1961	+ 16	+ 13
1962	+ 14	+ 10
1963	+ 12	+ 7
1959	+ 8	+ 7

Obviously, budworm development was significantly earlier in 1960 than in the other four years. This can be partly explained by early spring temperatures. For example, maximum daily temperatures were averaged for four weekly periods beginning on 15 May, and in 1960, these average weekly temperatures were 3.3°F, 12.7°F, 9.4°F, and 2.0°F above the overall average for the five years. The appearance of the first sixth-instar larva coincided, within 2 to 5 days, with the date when the current balsam fir shoots reached 50% of their total growth:

Year	First L6	50% shoot development	Difference in days
1961	28 June	3 July	+ 5
1962	26 June	28 June	+ 2
1963	24 June	27 June	+ 3

The density of third-instar larvae in expanding current shoots was selected as the 'starting' density. We did not use the second-instar density originally placed on the branch tips because no attempt was made to locate L2 that dispersed or were missed from the tagged branch. An estimate of the loss between second-instar larvae in mines and third-instar larvae in new shoots (on the same branch) for the period 1959-63 was as follows:

Year	No. of L2 in needle mines	No. of L3 in shoots	Percent loss
1959	462	367	20
1960	477	325	32
1961	422	369	13
1962	486	410	16
1963	490	388	21
Mean			20

It is impossible to say whether the 20% loss was an actual loss (predation, failure to find a suitable expanding bud) or if some larvae migrated and established on other branches. However, the data may also be interpreted as showing that the average loss of L2 from the needle mining stage to L3 in expanding current buds is unlikely to be greater than 20% on non-defoliated balsam fir. It is not known how this compares, for example, to the loss on late-developing hosts such as black spruce.

RESULTS AND DISCUSSION

The periodic recording of the number of living larvae in each experiment gave a series of population fixes from the third instar to the late pupal/adult stage (Tables 1, 2, 3).

Survival in Series 1 and 1A

The survival rate (L3 to adults) was high in the fine-mesh cages, ranging from 0.49 to 0.73:

Year	Survival rate L3-adult	
	Series 1	Series 1A
1959	0.71	
1960	0.70	
1961	0.73	
1962	0.62	0.70
1963	0.55	0.49

Mortality could be attributed to the following causes:

1. Missing. The number of larvae that could not be accounted for ranged from 0 to 20%. The mean, 11%, is not a high sampling error.
2. Disease. The major cause of mortality was classified as disease and the following table shows that survival in Series 1 and 1A was determined by the incidence of disease:

Ranked survivals in Series 1, 1A	Killed by disease (%)
0.73	12
0.71	4
0.70	7
0.70	13
0.62	16
0.55	23
0.49	27

Pathogens tend to kill late-instar larvae and pupae. Thus survival was high in the fine-mesh cages from L3 to peak L5 (averaging 0.90) and also high during the L5-L6 stage, averaging 0.92. The lowest mean survival, 0.85, was recorded during the peak L6 to adult stage when both larvae and pupae succumbed to disease.

Survival in Series 2

The survival rate (L3-adults) in the large-mesh cages was much lower than expected and ranged from 0.09 to 0.33:

Survival rate (L3-adults) in Series 2	
1959	0.09
1960	0.33
1961	0.33
1962	0.14
1963	0.15

Table 1. Population counts and mortality, Series 1, 1A

	Stage	Living larvae	Missing larvae	Dead		Parasitized
				Predation	Disease	
Series 1, 1959						
	L3	75	7	1		
	L5	67	2			
	L6	65	2	1	3	6
	Adults	53				
Series 1, 1960						
	L3	71		4	1	1
	L5	65		6	4	4
	L6	51		1		
	Adults	50				
Series 1, 1961						
	L3	73	4	3	5	
	L5	61	2			1
	L6	58	1		4	
	Adults	53				
Series 1, 1962						
	L3	37	2	1	3	
	L5	31			1	1
	L6	29	2	2	2	
	Adults	23				
Series 1, 1963						
	L3	40				
	L5	40	4	3	6	1
	L6	26		1	3	
	Adults	22				
Series 1A, 1962						
	L3	47	1	2	2	
	L5	42	1			
	L6	41	2	2	4	
	Adults	33				
Series 1A, 1963						
	L3	45	2		1	
	L5	42	6	1	7	
	L6	28	1	1	4	
	Adults	22				

Table 2. Population counts and mortality, Series 2

	Stage	Living larvae	Missing larvae	Dead		Parasitized
				Predation	Disease	
Series 2, 1959						
	L3	70	21	4	2	
	L5	43	16	4	3	9
	L6	11	1		1	3
	Adults	6				
Series 2, 1960						
	L3	72	1	8	1	1
	L5	61	13	6	2	7
	L6	33	5		4	
	Adults	24				
Series 2, 1961						
	L3	67		4	3	4
	L5	56	8	2		1
	L6	45	9	5	8	1
	Adults	22				
Series 2, 1962						
	L3	102	2	1	6	0
	L5	93	15	1	3	3
	L6	71	36	3	13	5
	Adults	14				
Series 2, 1963						
	L3	184	17	17	12	
	L5	138	40	1	13	4
	L6	80	16	1	26	10
	Adults	27				

Survival rate, L3 to L5

The survival rate from L3 to the peak L5 stage in the large-mesh cages was high and averaged 0.84. This compares to an average of 0.90 in the fine-mesh cages. The added mortality was classified as predation where apparently some small predators were able to penetrate the cage and attack small larvae.

Survival rate, L5 to L6

The survival rate in the large-mesh cages from the peak L5 to peak L6 averaged 0.66 compared to 0.92 in the fine-mesh cages. The major mortality factor was 'missing' larvae, averaging 23%. It became evident in the first year of the experiment with large-mesh cages that sixth-instar larvae were prone to migrate from their feeding sites and spin pupation sites on other parts of the branch. For example, in 1960 and 1961 only 38 and 28%, respectively, of the larvae that pupated did so in the sixth-instar feeding site. Many pupated on the cotton strip of the cage nearest the tree-trunk. The cause of this migration is only

Table 3. Population counts and mortality, Series 3

	Stage	Living larvae	Missing larvae	Dead		Parasitized
				Predation	Disease	
Series 3, 1959						
	L3	138	34	18	9	1
	L5	76	32	5	11	19
	L6	9	4			
	Adults	5				
Series 3, 1960						
	L3	117	23	14	7	10
	L5	63	12	17	13	13
	L6	8	5		1	
	Adults	2				
Series 3, 1961						
	L3	120	10	29	17	12
	L5	52	16	6	8	11
	L6	11	8		1	2
	Adults	0				
Series 3, 1962						
	L3	144	41	26	24	16
	L5	37	12	3	11	6
	L6	5	5			
	Adults	0				
Series 3, 1963						
	L3	175	44	38	15	3
	L5	75	24	5	28	10
	L6	8	2		5	1
	Adults	0				

partially understood but the contributing factors could have been

a) Too little current foliage. There appeared to be adequate current foliage in each cage but sixth-instar larvae may migrate before 100% defoliation occurs.

b) Low quality foliage. Although exposed foliage within the lower crown was caged, it did not have the same morphological characteristics as 'sun' foliage found near the top of the crown.

c) Radiant heat. The caged foliage was fully exposed to sunlight and the degree of heating may have caused a heat response (migration to shaded inner portion of the crown) among large larvae.

Although we refer to migration as the cause of missing larvae in the large-mesh cages we cannot ignore the possibility that large invertebrate predators could possibly have entered the cages and removed larvae. We saw no evidence of this. However, we did not carefully monitor large predators.

An attempt was made to monitor migration by placing a tray coated with an adhesive beneath the cage on the assumption that larvae might drop from the feeding site through the cage but no larvae were found in the trays. In some experiments a floor was placed in the cage but survival was not increased. Thus the sixth-instar larvae were lost from the large-mesh cages and their ultimate fate was not determined.

Survival rate, peak L6 to adults

The lowest survival rate in the large-mesh cages occurred during the peak L6 to the adult stage. The mean survival was 0.48 compared to 0.85 in the fine-mesh cage.

The major mortality factors were on average:

1. Missing - 17%
2. Parasitism - 10%
3. Dead larvae - Mainly disease increasing annually from 9% to 33%, averaging 22%.

Thus, the average survivals in the three age-intervals were 0.84 to 0.66, and 0.48 which, when multiplied give an L3 to adult survival of 0.27. This is somewhat lower than the recorded rate in 1960 and 1961 and higher than the rate in 1962 and 1963. The lower rates in 1962 and 1963 can be traced to a higher mortality caused by disease.

Survival in Series 3

In 3 of the 5 years of the study, none of the third-instar larvae on exposed branches survived to the adult stage. The major cause of mortality was 'missing' sixth-instar larvae and pupae.

Survival rate, L3 to L5

The average survival rate of exposed larvae from L3 to the peak of the fifth-instar was 0.44 as calculated from the following table:

Survival rate, L3-L5	
1959	0.55
1960	0.54
1961	0.43
1962	0.26
1963	0.43
Mean	0.44

The mortality factors were:

1. Disease - 4%
2. Small predators - 18%
3. Parasitism - 6%
4. Missing - 25%

Our interpretation of the 'missing' category is that during the L3 to L5 age-interval, 4% of the larvae in the fine-mesh cages were 'missed', 3% in the large-mesh cages, and therefore the 25% loss of exposed larvae represents a loss that we attribute to large invertebrate predators and/or birds.

Survival rate, L5-L6

The survival rate of exposed larvae from peak L5 to peak L6 was extremely low and averaged 0.14 as calculated from the following table:

Survival rate, L5-L6	
1959	0.12
1960	0.13
1961	0.21
1962	0.14
1963	0.11
Mean	0.14

The mortality factors were:

1. Missing - 32%
2. Parasitism - 19%
3. Dead - 32%, mainly disease.

The number of dead larvae classified as diseased was high among exposed larvae during the L5 to L6 age-interval and averaged 32%. The other major mortality factor was

'missing' larvae but we cannot attribute the 32% loss to bird predation because about the same loss, 23%, was recorded in large-mesh cages that excluded birds.

Survival rate, L6 to adults

With a survival rate of 0.44 during the L3-L5 stage and only 0.14 during the L5-L6 stage a simple calculation shows that only 6% of the exposed larvae survived to the peak of the sixth instar. A few of these survived to the adult stage in 1959 and 1960 but none in the other three years. Furthermore, in 1963 small larvae were confined in fine-mesh cages until the peak of sixth instar and then exposed in order to obtain a larger population of sixth-instar larvae. Even in this experiment none of the sixth-instar larvae survived. We can only conclude that exposed late sixth-instar larvae and pupae are highly vulnerable to natural mortality.

MORTALITY FACTORS

Parasitism A small chalid, Elachertus cacoeciae Howard, and an Apanteles sp. (very rare) were the only parasitic species recovered from experimental populations. This is an extremely simple complex as about 18 species were recovered from natural populations in the area. E. cacoeciae is an external parasite that lays two or more eggs per host and has been reared from a variety of Lepidoptera. It kills mainly fifth- and sixth-instar budworm larvae.

Parasitism among exposed larvae ranged from 8 to 25% (based on L3 densities) but there was no indication in the data that changes in the level of parasitism were associated with changes in L3 to adult survival rates.

Predation Small invertebrate predators attack and kill third-, fourth-, and fifth-instar larvae. Predation of exposed larvae during the L3-L5 age-interval was relatively constant and averaged 18%:

	Invertebrate predation of exposed larvae %
1959	13
1960	12
1961	24
1962	18
1963	22
Mean	18

Note that these data refer to small predators that did not remove larvae from the foliage.

Disease Dead larvae that appeared flaccid and discolored were classified as diseased. Some of the larvae were frozen and later examined microscopically. These examinations showed that pathogens could only be found in some of these larvae and it is assumed that the remainder died from inherent mortality.

Year	No. of larvae examined	Diseased %
1959	12	33
1960	42	48
1962	55	82
1963	56	32

Few third-and fourth instar larvae died from disease in 1959 and 1960 when larval development was relatively rapid. The percentage was much higher in the remaining years when development was slow under cool temperatures:

Percentage of hosts dying from disease in various stadia

	L3-L4	L5-L6	Pupa
1959	8	77	15
1960	9	79	12
1961	44	29	27
1962	49	42	07
1963	33	55	11

We had no reason to suspect that the percentage of larvae dying from disease and inherent mortality would differ in the three types of experiments. Yet, in general, we classified more dead larvae as diseased in the exposed population than among larvae in the fine-mesh cages:-

Percentage of budworm classified as diseased in the three series of experiments. Percentages based on third-instar density

	Series 1	1A	2	3
1959	4		9	14
1960	7		10	18
1961	12		16	22
1962	16	13	22	24
1963	23	27	28	27

In addition to the above differences in disease mortality between caged and exposed larvae we cannot explain the apparent annual increase in mortality caused by disease. If disease were closely correlated with unfavorable weather we would have expected maximum mortality in 1961. We can only conclude that disease (and inherent mortality) was the one factor most closely related to the changing survivals in the three series of experiments.

FECUNDITY

Late in the pupal development period, pupae were taken from the fine-mesh cages and the newly emerging adults were mated in single pair containers. The mean fecundities (Table 4) were surprisingly low as we expected a mean of close to 200. The actual fecundity may have been caused by poor quality current foliage in the lower branches of the crown even though such foliage was exposed to sunlight.

SUMMARY AND CONCLUSIONS

1. As expected, the survival rate during the peak third-instar to adult age interval was high in the fine-mesh cages. It averaged about 0.70. A small number of

Table 4. Fecundity of females taken from fine-mesh cages

Year	Number of females	Female emergence period	Fecundity Range	Mean
1960	12	7 - 19 July	63-238	135
1961	17	21 - 26 July	77-230	185
1962	25	24 July - 3 Aug.	60-205	137
1963	17	16 - 24 July	70-190	133

larvae, about 10%, were 'missing' from the foliage and about an equal percentage succumbed to small invertebrate predators and/or scavengers that managed to enter the cages. Most mortality was classified as disease that killed late-instar larvae and pupae.

2. Survival in the large-mesh cages was lower than expected, averaging about 0.30. The major mortality factor was 'missing' sixth-instar larvae that either migrated from their feeding sites and escaped from the cage or were removed by large invertebrate predators.
3. The primary aim in using large-mesh cages was to permit the entry of invertebrate predators and parasites and exclude birds. However, the experiment was poorly designed because (a) the cage hindered the attack of invertebrate predators and parasites (lower mortality among caged as compared to exposed larvae), and (b) 'missing' sixth-instar larvae made it impossible to identify mortality factors. The question of a better experimental design is not easily answered. Dowden et al. (1953) caged small trees with 0.6 cm screening and recorded the survival of late-instar larvae and pupae. In one year they could not account for 36% of the larvae, and the next year, 25%. This roughly compares to a 17% loss in our experiments. Whatever the cause(s) of this loss, some technique is required to identify it before bird predation among exposed larvae can be isolated from other mortality factors. If we had used the Dowden method of analysis (loss of larvae from exposed trees - loss of larvae from caged trees = bird predation) then we would have concluded that birds took about 80% of the few late sixth-instar larvae and pupae remaining on exposed branches. However, our data are too imprecise for such an analysis.
4. The analysis of invertebrate predation among exposed larvae showed that small invertebrate predators attacked third-, fourth-, and fifth-instar larvae and caused an average 18% mortality.
5. Disease and inherent mortality caused between 20 and 30% mortality in one year and there was evidence that increasing disease was associated with decreasing survival during the L3 to adult stage in all three series of experiments. This is one avenue where weather could play an indirect role in budworm dynamics.
6. The level of parasitism was generally low and was not related to changes in the L3 to adult survival rates.
7. When the peak third instar to adult age interval was subdivided into shorter periods all three series of experiments showed the lowest survival occurred during the peak L6 to adult period. Assuming that the peak L3 to adult age interval is the critical period in the dynamics of endemic populations then our data suggest that the fate of late fifth and sixth-instar larvae (mortality caused by disease, large invertebrate and bird predation) may be the key to population trends during the between-outbreak phase of the budworm cycle.

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