

POPULATION DYNAMICS OF THE LODGEPOLE NEEDLE MINER,  
 RECURVARIA STARKI FREEMAN, IN  
 CANADIAN ROCKY MOUNTAIN PARKS<sup>1</sup>

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Abstract

The lodgepole needle miner, *Recurvaria starki* Freeman, has been studied intensively since 1948. Life tables, survival, and death-rate curves show clearly that there are five periods in the 2-year life cycle of the needle miner during which extensive mortality may occur: (1) between egg formation and oviposition; (2) between oviposition and larval establishment; (3) during the first larval hibernation; (4) during the second larval hibernation; (5) during the spring of moth emergence. Population success is also undoubtedly affected by conditions during the adult life.

Population sampling has shown that the outbreak has declined since 1948. Defoliation and increment studies have shown that the period of greatest defoliation occurred from 1940 to 1944 and that the outbreak probably began in the late 1930's. The major cause of the decline was severe winter temperatures, probably during the coldest month. Parasitism was not an important factor in the outbreak decline, apparently because it was controlled in the same manner as the host, by winter temperatures. Other natural control factors are discussed as well as the possible effects of climatic factors on oviposition and fecundity.

A detailed survey of weather records since 1920 and yearly averages since 1885 suggest that release of the needle miner population was due to a warming trend in the climate of western Canada. This trend began in the late 1930's, reached a peak in the mid-1940's, and has declined since that time. The warming trend in northern latitudes has been noted by other authors and is substantiated by weather records of this region. It is further postulated that the climate of the Canadian Rocky Mountains is generally too severe for an outbreak of the lodgepole needle miner to be prolonged.

Introduction

The lodgepole needle miner, *Recurvaria starki* Freeman,<sup>3</sup> is a defoliator which attracted attention because of its increase in abundance in the Canadian Rocky Mountains during the 1940's. The forests attacked by this insect cover a vast western watershed and are the main forest stands in Banff, Yoho, Kootenay, and Jasper national parks.

The outbreak on which these studies are based was more extensive and severe in Banff Park than in other areas. *Pinus contorta* ssp. *latifolia* (Engelm. ex Wats.) is the sole host. The parks are similar physiographically: there is a relatively narrow valley in each with steep, high sides formed by mountain ranges of altitudes up to 10,000 ft. The direction of the valley is northwest in Banff, south in Kootenay, and west in Yoho. Timberline varies from 6500 ft to 8000 ft, being about 7200 ft in the Banff area. Valley bottom varies in

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<sup>3</sup>Publications prior to 1953 referred to this needle miner as *Recurvaria milleri* Busck and from 1953 to 1957 as *Recurvaria* sp.

altitude from 4000 ft at the eastern approaches to about 5000 ft at the Continental Divide. The main forest cover in the outbreak area consists of lodgepole pine stands of fire origin with an understory of spruce. Various age classes are represented but most stands are at least 80 years old.

The affected stands are adjacent to other extensive lodgepole pine stands of the eastern slopes of the Rocky Mountains in Alberta which form an important part of the province's forest industry. These considerations made it important to analyze the factors responsible for the increase in needle miner populations in the region, to explain zones of abundance within the outbreak, and to determine the factors which may limit outbreaks to the region recently affected. Since the late 1940's, needle miner populations have declined until at the present time (1959) high populations do not exist. This leads to the question whether such populations may recur although increment studies indicate that no previous outbreaks have occurred in this region during the life of the present timber stands. This paper is the third in a series dealing with various aspects of needle miner populations. The first (40) discussed sampling methodology and the second (42), the relation of climate to larval mortality of the needle miner. This paper describes the decline of the outbreak, outlining the control factors involved, and proposes a theory to explain the course of the outbreak. A subsequent paper describing the parasite complex and a discussion of parasite epidemiology is planned.

The needle miner in the Canadian Rockies has a 2-year life cycle (39). In the even-numbered years the adults emerge in July; eggs are laid in late July and August and hatch in August and September. Each larva immediately enters a needle in which it spends the first winter. The following spring, the miner commences to feed in late April or May, depending on spring weather, and completes the mining of the first needle. Transfer to a second needle takes place in mid-summer; climatic conditions affect the time and duration of the transfer period considerably. The larva overwinters in the second needle and the following spring, again an even-numbered year, transfers to a third needle. It completes mining by early June, pupates within the last mine, and the moth emerges 3 to 4 weeks later.

There have been three instances of out-of-phase populations. These are included in the life tables for 1958 as they were apparently part of the original established population. This proportion of the population was small and restricted in distribution, and no continuity of generations has been observed.

The outbreak was first noticed in June, 1942, on an area of approximately 50 square miles in Banff Park where it joins Kootenay Park at Vermilion Summit. The attack was largely confined to elevations between 5000 and 6500 ft (5). By 1944 it had spread into Yoho and Kootenay parks for short distances (18) and by 1946 it was estimated to cover 300 sq. miles, mostly in Banff Park (14). Populations had also increased in numbers below the 5000 ft levels, extending into the valley bottom (13). The outbreak covered an area of 400 sq. miles by 1948 (21) and a second outbreak in Jasper National Park

was reported on the slopes below Mount Edith Cavell (22, 37). This was entirely separate from the more southerly outbreak and was considered autochthonous (8).

### Life Tables for the Lodgepole Needle Miner

The formulation and use of life tables for needle miner epidemiological studies have been described (40). The sampling unit upon which the life tables were based is the number of individuals per 5-year branch tip (38). This is expressed under the  $lx$  column as the number of individuals per 100 branch tips. Six sampling periods: one egg, four larval, and one pupal, were deemed suitable to assess the course of a single generation from the time of oviposition to moth emergence (40). Each stage is sampled until the mean number of needle miners found, regardless of condition, agrees with the estimate from the previous sample (error limits,  $\pm 10\%$  of the mean). The total number of dead larvae is derived by subtracting the number of live larvae found (in sample) from the previous sample. The number attributed to any single mortality factor is calculated from the percentage mortality caused by that factor. The estimates are rounded and apportioned to the known mortality factors so that the life table is subtractive throughout. The following four areas are being sampled regularly for additional life table data:

(1) *Mount Eisenhower, Banff National Park*.—The sample area is located 22 miles northwest of the town of Banff, Alberta, on the east side of the Bow Valley. The elevation sampled is 5400 ft, 750 ft above valley bottom (Tables I and II, Figs. 1 and 2).

(2) *Massive Range, Banff National Park*.—This area is located about 11 miles northwest of Banff on the west side of the Bow Valley. The stands sampled are at approximately 5400 ft elevation, 600 ft above valley bottom (Tables III and IV, Figs. 3 and 4).

(3) *Mount Girouard, Banff National Park*.—The area sampled is located about 9 miles northeast of Banff on the south side of Lake Minnewanka. The samples are taken at approximately 6000 ft, 700 ft above valley bottom (Tables V and VI, Figs. 5 and 6).

(4) *Mount Cathedral, Yoho National Park*.—This area is located on a north-facing slope about 250 ft from valley bottom, elevation 4950 ft. It is approximately 6 miles from the Continental Divide (Tables VII and VIII, Figs. 7 and 8).

Two methods have been used in attempts to determine moth fecundity: controlled matings and moth dissections. Attempts to mate needle miner moths have been only partially successful; perhaps flight is necessary prior to copulation. Moth dissections made over the period 1950 to 1958 gave some measure of the minimum number of eggs that needle miner moths are capable of laying. The number of eggs used to calculate the expected number in all areas was 12 to 37. This range encompasses all previous estimates but observations lead the author to believe that the actual numbers laid are in the bottom of this range.

TABLE I<sup>1</sup>  
Life table for the 1954-1956 generation of needle miner,  
Mount Eisenhower (5400-ft elevation)

<i>X</i>	<i>lx</i>	<i>dxF</i>	<i>dx</i>	100 <i>qx</i>
<i>X</i> <sub>1</sub> : eggs, July, 1954	4700	Needle drop and unknown Resination	3586 0	76.30
			3586	76.30
<i>X</i> <sub>2</sub> : I and II instars, Sept., 1954	1114	Winter mortality	409	36.68
Extra: Dec. 14, 1954	705	Winter mortality Spring mortality Out-of-phase larvae	219 70 0	31.06 9.93 —
			289	40.99
<i>X</i> <sub>3</sub> , <i>X</i> <sub>4</sub> : III and IV instars, July, 1955	416	Winter mortality Spring mortality Bird predation Unknown	143 0 0 8	34.37 — — 1.98
			151	36.35
<i>X</i> <sub>5</sub> : IV and V instars, May, 1956	265	Larval parasitism	160	60.38
<i>X</i> <sub>6</sub> : Pupae, June, 1956	105	Pupal parasitism Unknown pupal mortality Moths trapped in needles	<1 26 0	0.45 24.76 —
			26+	25.21
Emergents	79			
Sex ratio 52:48	41F 38M			
Generation mortality			4621	98.32
Expected number of eggs	= 456-1406			
Measured number	= 378	Population trend = 8.0%		
Number of larvae established	= 308	Population trend = 27.5%		

<sup>1</sup>Table headings: *X*, stage at which sample is taken; *lx*, the number surviving at the beginning of the stage noted in the *X* column; *dxF*, the mortality factor responsible for *dx*, the number dying within the interval between successive samples; 100 *qx*, percentage mortality. The 'population trend' is the percentage calculated by comparing the number of eggs or larvae of the new generation to those at the beginning of the *lx* column.

## Natural Control Factors

### CLIMATIC FACTORS

#### (1) Winter Mortality

"Cold death" of insects has been extensively reported on in the literature, including various examples of the control of insect populations (3, 6, 10, 17, 20, 23, 30). Limited tests on lodgepole needle miner larvae in the laboratory indicated that they are extremely cold-hardy, even in the immature stages. Tests on first-instar larvae, in August and September, demonstrated that they could withstand temperatures of 21° F for periods up to 24 hours; temperatures of 0° F caused no mortality in 1 hour but almost 100% mortality in 24 hours. Dissections of third- and fourth-instar larvae in November

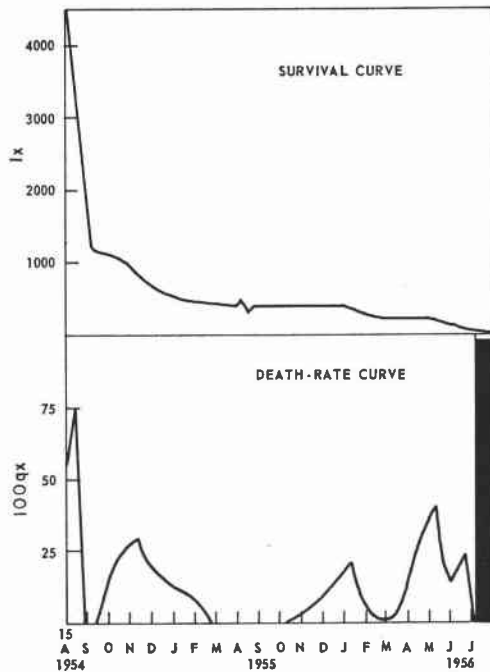


FIG. 1. Survival and death-rate curves; Mount Eisenhower, valley bottom plus 750 ft (5400 ft), 1954-56 generation.

indicated that they hibernate with no food in the gut, thereby increasing their cold resistance (32). No significant mortality was observed at temperatures maintained at  $-8^{\circ}\text{F}$  for 24 hours. A detailed discussion of the relation of climate to winter mortality is presented in a previous report (42). It was demonstrated, from a comparison of winter mortality estimates, that larval populations can have a high survival if January minimum temperatures of  $-30^{\circ}\text{F}$  to  $-40^{\circ}\text{F}$  do not persist long enough to depress the mean monthly temperature to the zero mark or if the weather is not abnormally severe in other winter months.

There appears to be little doubt that winter temperatures have been the main cause for the decline in needle miner populations. High mortality was first observed in 1946 (13) but populations were still high until the winter of 1949-50 (11). Since 1950 the population has been reduced (in numbers) and has been restricted to the intermediate levels on the mountain slopes where it was first noted. The percentage mortality for the whole generation is more significant when based on the first-instar larval population than those based on yearly estimates of the population present before hibernation (Table IX). A detailed discussion of year-to-year variations of winter mortality has been presented elsewhere (42).

The importance of winter mortality is clearly shown when compared with other control factors (Fig. 9). Estimates of average parasitism for comparable

TABLE II  
Life table for the 1956-1958 generation of needle miner,  
Mount Eisenhower (5400-ft elevation)

<i>X</i>	<i>lx</i>	<i>dxF</i>	<i>dx</i>	100 <i>qx</i>
<i>X</i> <sub>1</sub> : eggs, July, 1956	378	Needle drop	61	16.14
		Resination	9	2.38
			70	18.52
<i>X</i> <sub>2</sub> : I and II instars, Sept., 1956	308	Winter mortality	36	11.69
		Spring mortality	0	—
		Out-of-phase larvae	11	3.57
			47	15.26
<i>X</i> <sub>3</sub> , <i>X</i> <sub>4</sub> : III and IV instars, July, 1957	261	Winter mortality	14	5.36
		Spring mortality	11	4.21
		Others including bird predation	2	0.77
			27	10.34
<i>X</i> <sub>5</sub> : IV and V instars, May, 1958	234	Larval parasitism	95	40.59
<i>X</i> <sub>6</sub> : Pupae, June, 1958	139	Pupal parasitism	0	
		Unknown pupal mortality	8	5.76
		Moths trapped in needles	3	2.16
			11	7.92
Emergents	128			
Sex ratio 47:53	60F 68M			
Generation mortality			250	66.14
Expected number of eggs	= 720-2220			
Measured number	= 328	Population trend = 86.8%		
Number of larvae established	= 215	Population trend = 69.8%		

areas were divided between the two generation years to make them comparable to winter mortality, for which yearly estimates are available, i.e. they are additive. All other mortality factors, excluding those acting on the egg population, are combined; data on these factors are available from 1955 to 1958. For the years measured it would appear that parasitism was controlled in a manner similar to population, at least up to the 1956-58 generation.

### (2) Spring Mortality

A small percentage of larvae killed after feeding each spring has been found since detailed sampling for life table studies was commenced in 1954. This mortality never exceeded 8% of the larval population entering hibernation. It has long been recognized that spring mortality can be an important factor, particularly in open-feeding insects (4, 12, 52). Early studies on the needle miner indicate that the commencement of feeding in the spring is largely dependent on spring temperatures. Generally it appears that feeding ceases

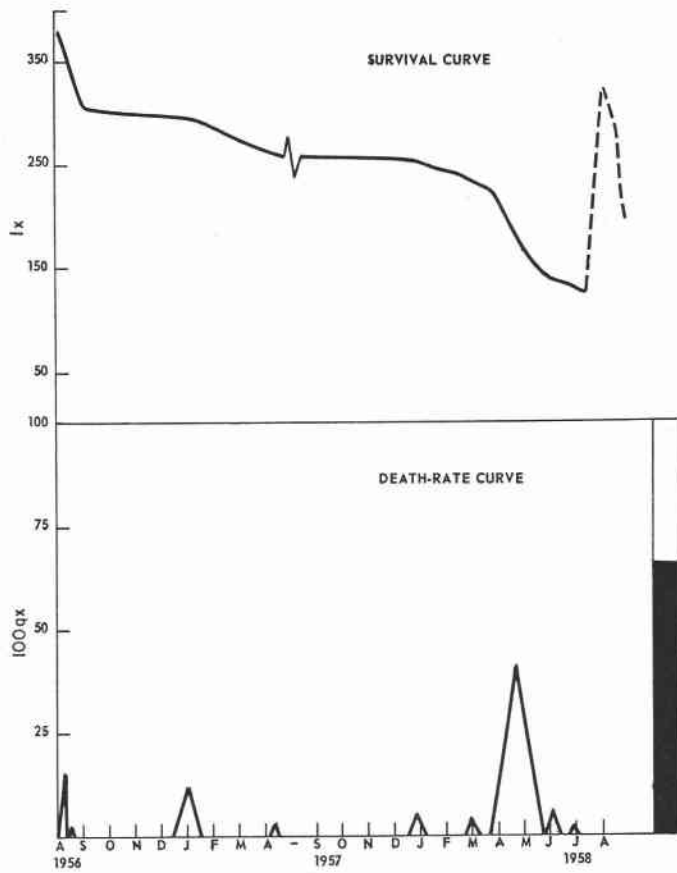


FIG. 2. Survival and death-rate curves; Mount Eisenhower, valley bottom plus 750 ft (5400 ft); 1956-58 generation.

in the fall when maximum temperatures fall below 45° F and the minimum temperatures are commonly below freezing. The reverse of these conditions is associated with commencement of spring feeding (37). Spring frosts are common and may be severe enough to cause the mortality observed.

### (3) Possible Mortality from Other Climatic Factors

#### (a) Eggs and First-instar Larvae

No mortality of eggs in the field or laboratory has been observed. They are apparently able to endure any field condition which occurred in the 3 years that egg sampling was carried out. However, large reductions in populations between oviposition and larval establishment may occur periodically. This was shown in 1954 when a count of 4700 eggs per 100 tips was made and establishment was only 1114 larvae per 100 tips.

Two sources of loss have been observed in the field but techniques have not been designed by which they can be evaluated except by subtraction from

TABLE III  
Life table for the 1954-1956 generation of needle miner,  
Massive Range (5500-ft elevation)

	$lx$	$dxF$	$dx$	100 $qx$
$X_1$ : eggs	Not measured			
$X_2$ : I and II instars, Sept., 1954	1257	Winter mortality	737	58.60
		Spring mortality	55	4.38
		Out-of-phase larvae	0	
			792	62.98
$X_3, X_4$ : III and IV instars, July, 1955	465	Winter mortality	94	20.22
		Spring mortality	2	0.43
		Bird predation	124	26.67
			220	47.32
$X_5$ : IV and V instars, May, 1956	245	Larval parasitism	123	50.20
$X_6$ : Pupae, June, 1956	122	Pupal parasitism	0	
		Unknown pupal mortality	30	24.84
		Moths trapped in needles	0	
			30	24.84
Emergents	92			
Sex ratio 55:45	51F 41M			
Generation mortality			1165	92.68
Expected number of eggs = 492-1517				
Measured number—inadequate sample		Population trend—unknown		
Number of larvae established = 190		Population trend = 15.1%		

present sampling stages. One of these is the drop of mined needles containing eggs, and the other is the prevention of larval establishment by adverse weather factors. Examination of the needle litter at the base of trees has substantiated that drop of mined needles containing eggs does occur occasionally. Morgan (25) estimated this loss to be 18% in the California needle miner in 1955. Since loss of eggs did not occur in the Bow Valley in 1956 or 1958, it is probable that this form of loss is intermittent, perhaps resulting from strong gusts of wind during the time of egg development. No measurement has been made of the loss of first-instar larvae but it is recognized that it could be an important factor in population reduction. Experiments by Shepherd (34) indicated that the threshold of activity of newly emerged larvae is rather high (59-65° F), and limited experiments indicated that high humidities restrict first-instar larval activity. Examination of hygrothermograph records in 1954 indicate a cold, wet period from August 18 to 24 which corresponds closely to the hatching period. Again, no measurement of loss is possible except by subtraction in the life table but it is reasonably certain that the combination of low temperature and high humidity is at least partly responsible for the loss noted in 1954 between oviposition and larval establishment. This loss did not



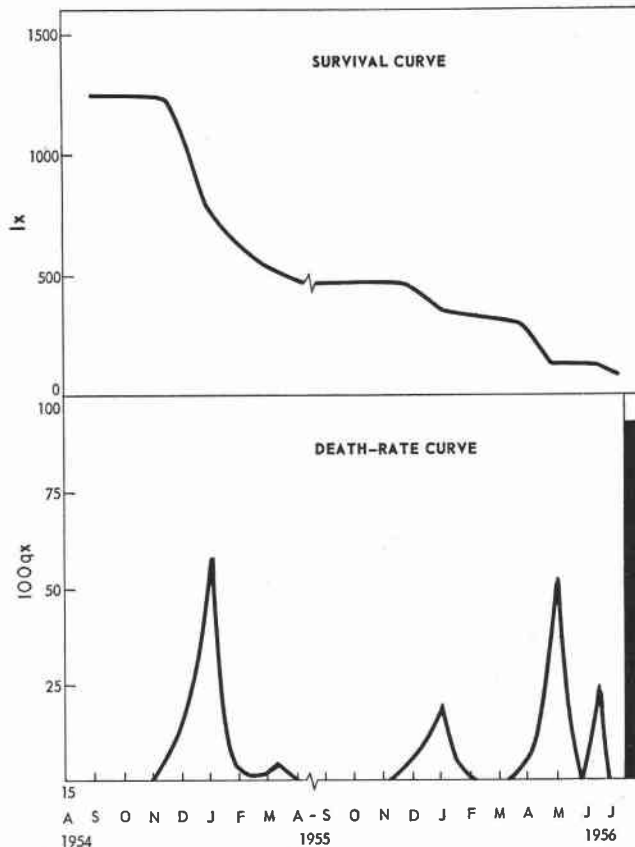


FIG. 3. Survival and death-rate curves; Massive Mountain, valley bottom plus 600 ft (5500 ft); 1954-56 generation.

occur in 1956, in which year conditions were more favorable for larval establishment (41).

(b) *Larvae during the Summer*

The suggestion by Morgan (25) that needle miner larvae are forced from their mines by excessive heat has not been observed under Canadian conditions. Although mortality has not been found during summer when only larvae are present, adverse climatic factors during this period may have a long-term effect on the population by influencing larval development. For example, the cool, wet summer of 1951 in Yoho Park extended the normal time for larval transfer from first to second needles by 2 to 3 weeks. Such a delay in larval transfer could reduce populations by its effects on winter survival and possibly on fecundity.

(c) *Pupae*

The mortality of pupae in all areas except Mount Cathedral in Yoho Park was estimated at from 20 to 25% in 1956 and as high as 40% in 1958. The cause of pupal mortality is unknown but is believed to be of climatic origin.

TABLE IV  
Life table for the 1956-1958 generation of needle miner,  
Massive Range (5500-ft elevation)

<i>X</i>	<i>lx</i>	<i>dxF</i>	<i>dx</i>	100 <i>qx</i>
<i>X</i> <sub>1</sub> : Eggs, July, 1956	Inadequate sample			
<i>X</i> <sub>2</sub> : I and II instars, Sept., 1956	190	Winter mortality	30	15.79
		Spring mortality	6	3.16
		Out-of-phase larvae	3	1.58
			39	20.53
<i>X</i> <sub>3</sub> , <i>X</i> <sub>4</sub> : III and IV instars, July, 1957	151	Winter mortality	23	15.23
		Spring mortality	13	8.61
		Bird predation	1	0.66
		Unknown	52	34.44
			89	58.94
<i>X</i> <sub>5</sub> : IV and V instars, May, 1958	62	Larval parasitism	29	46.77
<i>X</i> <sub>6</sub> : Pupae, June 1958	33	Pupal parasitism	0	
		Unknown pupal mortality	10	30.30
		Moths trapped in needles	3	9.09
			13	39.39
Emergents	20			
Sex ratio 58:42	12F 8M			
Generation mortality			170	89.47
Expected number of eggs	= 96-296			
Measured number—inadequate sample		Population trend—unknown		
Number of larvae established	= 195	Population trend = 102.2%		

(d) *Adults*

The separate activities of flight and oviposition, as well as fecundity and fertility, were considered together in relation to abundance of adults. Detailed information on this stage is available for only three generations: 1954, 1956, and 1958. While estimates of potential population are admittedly crude, some workers have shown by dissection that minimum egg potential approaches 100 eggs per female (unpublished data) but for the present purposes 12 to 37 eggs are used. The choice of this range was based partly on the results of recent moth dissections and egg-sampling results. Fecundity may be adversely affected by conditions during the developmental period (33, 52) and field samples indicate that fewer eggs are laid than is usually expected. No abnormalities of ovaries were observed in moths.

Pairing of captive adults was largely unsuccessful, but for those females that did lay eggs the range was from 1 to 19, the average only 8 eggs per female. Field sampling, where successful, indicated an average of about 8 eggs per female also. Field observations and population sampling indicated that the number of eggs laid, at least in the last two moth flights, is lower

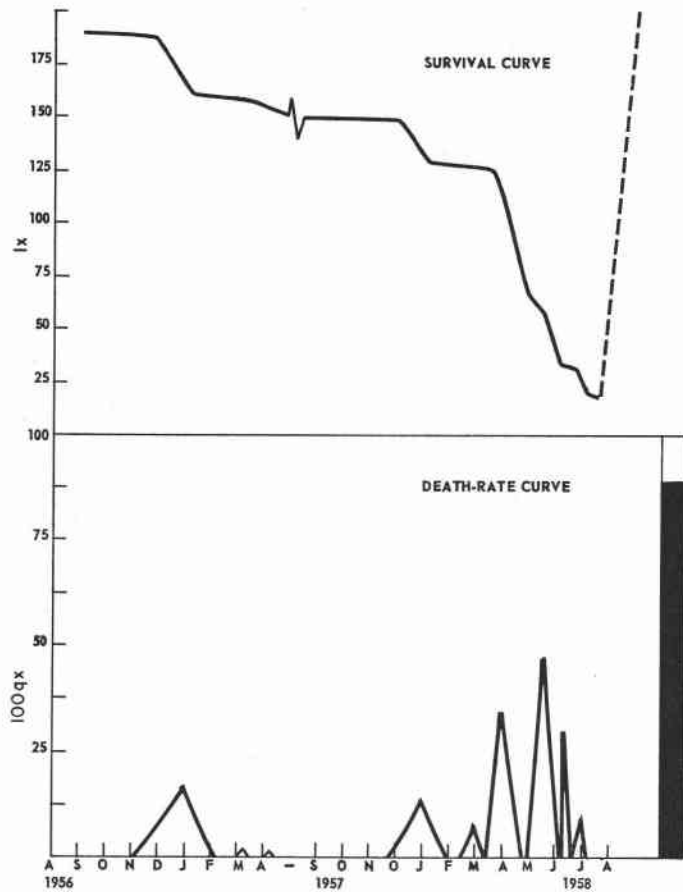


FIG. 4. Survival and death-rate curves; Massive Mountain, valley bottom plus 600 ft (5500 ft); 1956-58 generation.

than the bottom of the estimated range. Oviposition is very easily disrupted and this could be a very significant factor in population reduction, depending largely on the weather during the egg-laying period. Possibly greater inhibition of oviposition in 1956 and 1958 than in 1954 was indicated by egg samples, since fewer large egg masses were found in these later years than in 1954 and the number of single eggs found in proportion to the total number was far greater.

Cold, windy, or rainy weather has an important effect on moth flight and oviposition. Field observations in 1956 and 1958 indicated that moths did not lay at temperatures below 45° F and at wind speeds above 3 to 5 m.p.h. Another less obvious effect was observed in 1958 when a very severe storm, accompanied by high winds and heavy rain, occurred during the moth flight between the emergence times of males and females. Normally males emerge first, the proportion of males to females becoming about equal approximately

TABLE V  
Life table for the 1954-1956 generation of needle miner,  
Mount Girouard (6000-ft elevation)

<i>X</i>	<i>lx</i>	<i>dxF</i>	<i>dx</i>	100 <i>qx</i>
<i>X</i> <sub>1</sub> : eggs, not measured				
<i>X</i> <sub>2</sub> : I and II instar, Sept., 1954	2633	Winter mortality Spring mortality Out-of-phase larvae	1593 144 0	60.50 5.46
			1737	65.96
<i>X</i> <sub>3</sub> , <i>X</i> <sub>4</sub> : III and IV instars, July, 1955	896	Winter mortality Spring mortality Bird predation Unknown	213 15 76 41	23.77 1.67 8.50 4.60
			345	38.54
<i>X</i> <sub>5</sub> : IV and V instars, May, 1956	551	Larval parasitism	288	52.27
<i>X</i> <sub>6</sub> : Pupae, June, 1956	263	Pupal parasitism Unknown pupal mortality Moths trapped in needles	2 56 0	7.60 21.29
			58	28.89
Emergents	205			
Sex ratio 53:47	109F 96M			
Generation mortality			2428	92.21
Expected number of eggs	= 1152-3552			
Measured number	= 385	Population trend—unknown		
Number of larvae established	= 395	Population trend = 14.6%		

2 weeks after the beginning of emergence. Such a storm, occurring when a preponderance of males was present, could have reduced the male population to a point where many of the females would not be mated. Factors such as outlined above could explain the continued decline in population even though winter mortality, parasitism, and other factors were low (Fig. 9).

The moths are crepuscular. Diminution of light (or radiation), such as occurs during cloudy periods, caused increased activity during the day. Peak flight activity is at sunset, provided there is no wind or rain, the moths flying upwards to the tops of the tree crowns, giving rise to the distribution of eggs and larvae found (38). While fluctuations in barometric pressure caused increased flight activity in some insects (44, 53) this did not appear to be a factor influencing needle miner flight activity.

#### PARASITISM

This paper considers only the total role of parasites in the dynamics of the past outbreak of the lodgepole needle miner. Information on parasite biologies and dynamics and the breakdown of the parasite complex by species in supplementary life tables is planned for a separate publication.

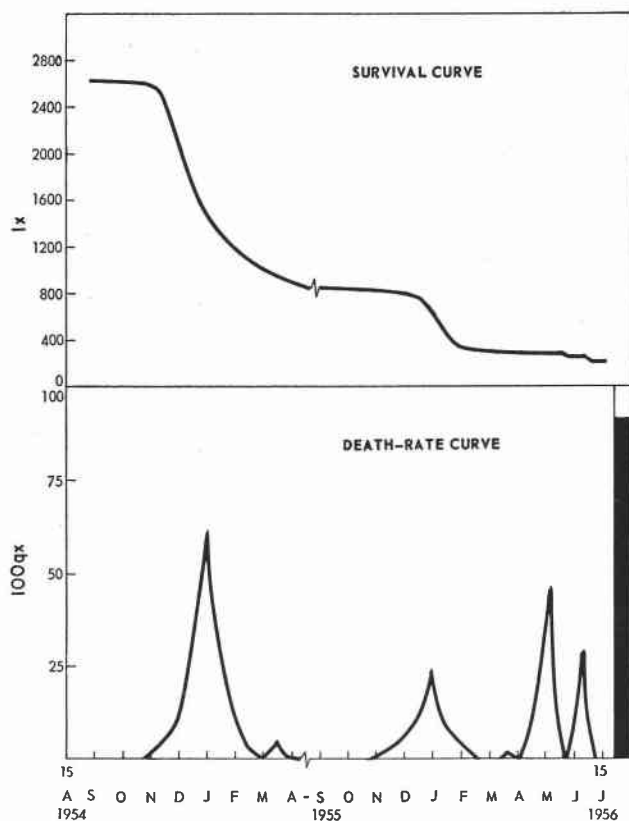


FIG. 5. Survival and death-rate curves; Mount Girouard, valley bottom plus 700 ft (6000 ft); 1954-56 generation.

Parasites have long been upheld as the major influence in so-called "biotic" control and many instances have been cited where economic control has been effected, largely through the introduction of parasites. Sweetman (45) subjected many stated examples to intense scrutiny and concluded that many of these were attributable to factors other than biotic. Andrewartha and Birch (2) and Milne (24) point out that there are few or no proved cases of control of an insect population by its parasites and that abundant evidence exists that they are unable to do so. The current study recognizes the possibility of control through parasites, at least to the extent of gaining an understanding of them as they affect the dynamics of needle miner populations.

It has been shown (Fig. 9) that parasitism was not as important a factor as winter mortality when compared with total population, for any generation except 1956-58, and did not play an important part in reducing needle miner populations. In fact, parasitism appeared to be controlled by climate in the same manner as was the needle miner population. However, parasitism achieves considerable importance in the later part of the life cycle when its effect on the population surviving the two winters is considered (Table X).

TABLE VI  
Life table for the 1956-1958 generation of needle miner,  
Mount Girouard (6000-ft elevation)

<i>X</i>	<i>lx</i>	<i>dxF</i>	<i>dx</i>	100 <i>qx</i>
<i>X</i> <sub>1</sub> : eggs, July, 1956	385	Needle drop Resination	0 0	
<i>X</i> <sub>2</sub> : I and II instar, Sept., 1956	395	Winter mortality Spring mortality Out-of-phase larvae	126 18 32	31.90 4.56 8.10
			176	44.56
<i>X</i> <sub>3</sub> , <i>X</i> <sub>4</sub> : III and IV instars, July, 1957	219	Winter mortality Spring mortality Bird predation and unknown mortality	15 0 < 1	6.85  < .01
			15+	6.85
<i>X</i> <sub>5</sub> : IV and V instars, May, 1958	204	Larval parasitism	111	54.41
<i>X</i> <sub>6</sub> : Pupae, June, 1958	93	Pupal parasitism Unknown pupal mortality Moths trapped in needles	0 38 6	40.86 6.45
			44	47.31
Emergents Sex ratio 46:54	49 23F 26M			
Generation mortality			346	87.59
Expected number of eggs = 276-851				
Measured number = 327		Population trend = 84.9%		
Number of larvae established = 334		Population trend = 84.6%		

Estimates of parasitism are probably low as there is no way of determining mortality from parasitism in the early stages of the host except by internal examination of needle miner larvae. Practical considerations do not permit such sampling at present. When the actual numbers of parasites are compared on the same basis as for the host (number per branch tip) it is evident that the actual number of parasites is declining but at a slower rate than the host (Fig. 9). The possibility exists that the parasite complex of the lodgepole needle miner, *Recurvaria starki* Free., has been kept at low levels of abundance during the past needle miner outbreak by a combination of factors which permitted host increase but inhibited parasite success.

#### PREDATION

No significant loss in eggs or larvae could be attributed to predation at any time prior to 1956. Predation of eggs has not been observed and only limited and localized predation of larvae by birds is believed to occur. Numerous needles that had been shredded, presumably by birds, were noted in two areas in 1956, Mt. Girouard and Massive, but predation was again negligible in

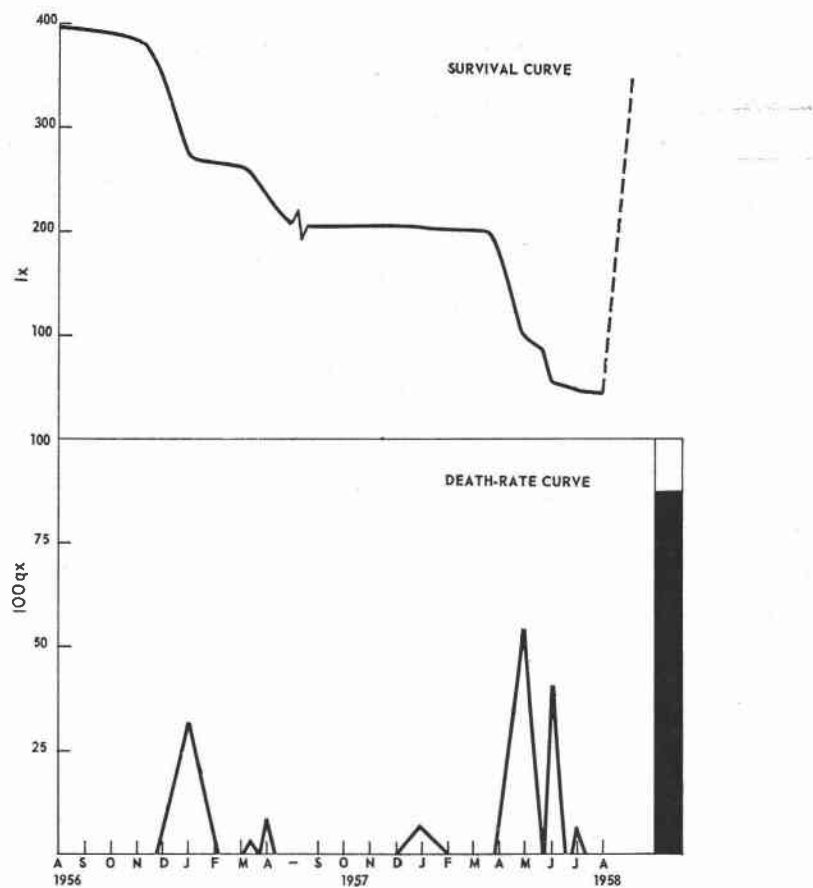


FIG. 6. Survival and death-rate curves; Mount Girouard, valley bottom plus 700 ft (6000 ft); 1956-58 generation.

1958. The most probable predators were chickadees, Rocky Mountain jays, and juncos. The importance of predation in the dynamics of needle miner populations, while difficult to assess, is believed to be low. On the other hand, predation could assume greater importance at times when needle miner populations are low and restricted to distinct refuge areas.

#### DISEASE

Disease has not been an important factor in the needle miner outbreak. The occurrence of diseased larvae reported in 1945 and 1946 (13) is now in doubt; winter-killed larvae were mistaken for diseased ones (Hopping, G.R., personal communication). Disease was not apparent before 1952 and since that time only a few diseased larvae have been detected. Adults have been similarly disease-free. A virus disease was isolated from the California needle miner in 1952 but attempts to introduce this into the Canadian population failed (unpublished data).

TABLE VII

Life table for the 1954-1956 generation of needle miner,  
Cathedral Mountain (4700-ft elevation)

$X$	$lx$	$dxF$	$dx$	100 $qx$
$X_1$ : eggs, not measured				
$X_2$ : I and II instars, Sept., 1954	924	Winter mortality	687	74.40
		Spring mortality	56	6.02
		Out-of-phase larvae	0	—
			743	80.42
$X_3, X_4$ : III and IV instars, July, 1955	181	Winter mortality	111	61.33
		Spring mortality	6	3.31
		Bird predation and unknown	0	—
			117	64.64
$X_5$ : IV and V instars, May, 1956	64	Larval parasitism	22	34.38
$X_6$ : Pupae, June, 1956	42	Pupal parasitism	0	
		Unknown pupal mortality	0	
		Moths trapped in needles	0	
Emergents	42			
Sex ratio: 49:51	21F 21M			
Generation mortality			882	95.45
Expected number of eggs	= 252-777			
Measured number—inadequate sample		Population trend—unknown		
Number of larvae established	= 66	Population trend = 7.1%		

## OTHER NATURAL CONTROL FACTORS

(1) *Resination*

Behavior of first-instar larvae of *Recurvaria starki* Free. and *R. milleri* Busck is almost identical. Upon eclosion they seek a green needle and begin to mine, almost invariably on the convex or outer surface of the needle (31, 39). The few that attempt to enter the needle from the concave or inner surface are usually killed. The abortive mine frequently has a small bubble of resin above it with the remains of the larva imbedded in the resin. The larval loss in the Canadian population has been negligible. Morgan (25) found similar mortality in California and estimated that 0.1% of the larval population died this way.

(2) *Competition and Overpopulation Factors*

There is no evidence to suggest that any other organism competes with the lodgepole needle miner for its food. The needle miner populations in the Canadian outbreak never reached the levels which would cause a critical food shortage. Intensive defoliation analyses that were begun in 1949 showed that populations did not persist at high levels long enough to cause complete defoliation. However, populations from 1940 to 1948 were high enough to cause about 80% defoliation in some localities and had these populations per-



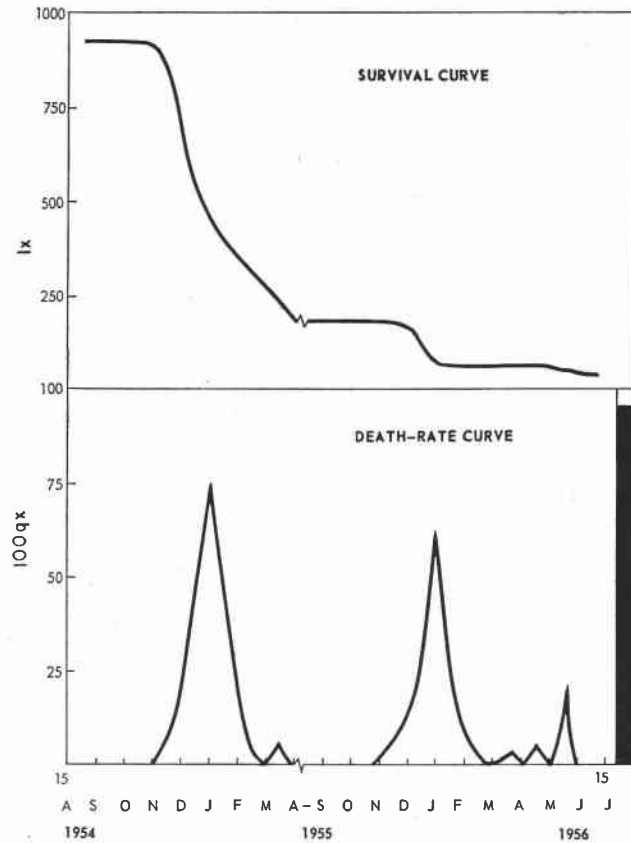


FIG. 7. Survival and death-rate curves; Cathedral Mountain, valley bottom plus 250 ft (4700 ft); 1954-56 generation.

sisted, food shortages would have occurred in localized areas (43). In this outbreak, therefore, competition is discounted as a significant population reduction factor.

"Overpopulation" factors (7, 35) have been credited by various authors with causing fluctuations in forest insect pests. However, the closely allied California needle miner has repeatedly reached the saturation point of its environment, killing forests over large areas without noticeable reduction in population prior to their own starvation and death. Survivors from those populations which caused total defoliation have caused outbreaks in new locations (25, 31).

### Epidemiology

#### THE THEORY OF CLIMATIC RELEASE

The importance of climate in the epidemiology of insect outbreaks has been a subject of controversy for many years. Early theories place the emphasis on biotic factors but some authors recognized that weather may cause an

TABLE VIII

Life table for the 1956-1958 generation of needle miner,  
Cathedral Mountain (4700-ft elevation)

<i>X</i>	<i>lx</i>	<i>dxF</i>	<i>dx</i>	100 <i>qx</i>
<i>X</i> <sub>1</sub> : eggs, July, 1956	Inadequate sample			
<i>X</i> <sub>2</sub> : I and II instars, Sept., 1956	66	Winter mortality	22	33.33
		Spring mortality	0	
		Out-of-phase larvae	14	21.21
			36	54.54
<i>X</i> <sub>3</sub> , <i>X</i> <sub>4</sub> : III and IV instars, July, 1957	30	Winter mortality	2	6.67
		Spring mortality	2	6.67
		Bird predation	<1	0.73
		Unknown	<1	2.60
			5	16.67
<i>X</i> <sub>5</sub> : IV and V instars, May, 1958	25	Larval parasitism	10	40.00
<i>X</i> <sub>6</sub> : Pupae, June, 1958	15	Pupal parasitism	0	
		Unknown pupal mortality	3	20.00
		Moths trapped in needles	1	6.69
			4	26.69
Emergents	11			
Sex ratio 60:40	7F 4M			
Generation mortality			55	83.33
Expected number of eggs	= 48-148			
Measured number	= 35	Population trend—unknown		
Number of larvae established	= 36	Population trend = 54.6%		

"unbalance" which may lead to outbreaks (35). Later theories were more comprehensive (33, 36). Nicholson (27, 28, 29) believes that populations are in a state of balance and the main controlling factors (of numbers) are "density-dependent", a condition which includes direct competition for resources or space and parasites, predators, and pathogens. He claims that climate is "density-independent" and can never control populations. Andrewartha and Birch (2) hold that the factors of environment that control insect populations are numerous but that climatic factors are of major importance. They conclude that all factors are "density-dependent" and attach no special importance to biotic factors. Thompson (48, 49, 50) believes that natural control results from an organism living in a continuously fluctuating environment. Under favorable conditions, numbers increase; under unfavorable conditions, numbers decrease. Never do numbers increase indefinitely and rarely if ever, decrease to extinction. Fluctuations in population numbers tend to be inversely correlated with the complexity of the "ecosystem", a view held by many authors (1, 2, 16). Milne (24) reviewed the theories mentioned above and proposes his own, which he describes as a "modification of Thompson's".

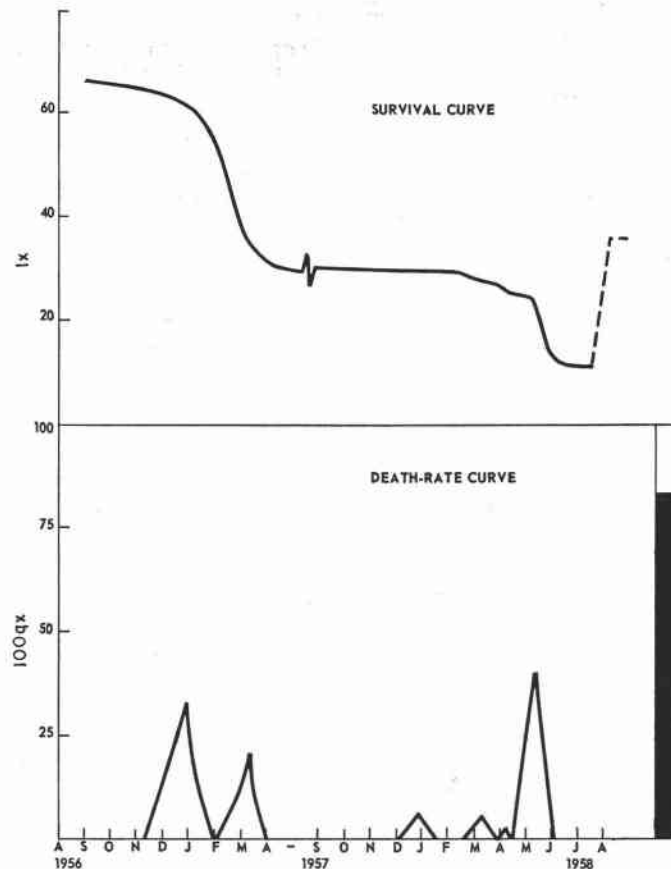


FIG. 8. Survival and death-rate curves; Cathedral Mountain, valley bottom plus 250 ft (4700 ft); 1956-58 generation.

He objects to the Nicholson theory on the grounds that competing species, parasites, predators, and pathogens can not control because they are "imperfectly density-dependent" and to Thompson's theory that it underestimates the importance of density-dependence. He also claims that the Andrewartha and Birch theory suffers from their treatment of density-dependence. Milne's own theory is that competition between individuals of a single species is "the only perfectly density-dependent factor" in nature. This factor is seldom evoked and therefore the control of increase is the combined action of factors, density-independent and "imperfectly" density-dependent. The control of decrease of numbers is brought about by density-independent factors.

Ulyett (51) has called climate a "catastrophic" factor and thinks it can be a contributory cause to insect outbreaks. This is based on the assumption that "density-dependent" (biotic) factors are more adversely affected by such catastrophes than the insect in question. In the absence of these controlling factors the insect may reach destructive densities when the catastrophe is

TABLE IX

Winter mortality of lodgepole needle miner: per cent mortality of whole generation based on number of established first-instar larvae

Area	Year				
	1948-50	1950-52	1952-54	1954-56	1956-58
Mt. Eisenhower, valley bottom	85	—	99	100	—
Mt. Eisenhower, 5400 ft	78	33	45	70	21
Massive	—	—	—	73	45
Girouard	—	—	—	86	60
Cathedral	—	—	—	68	65

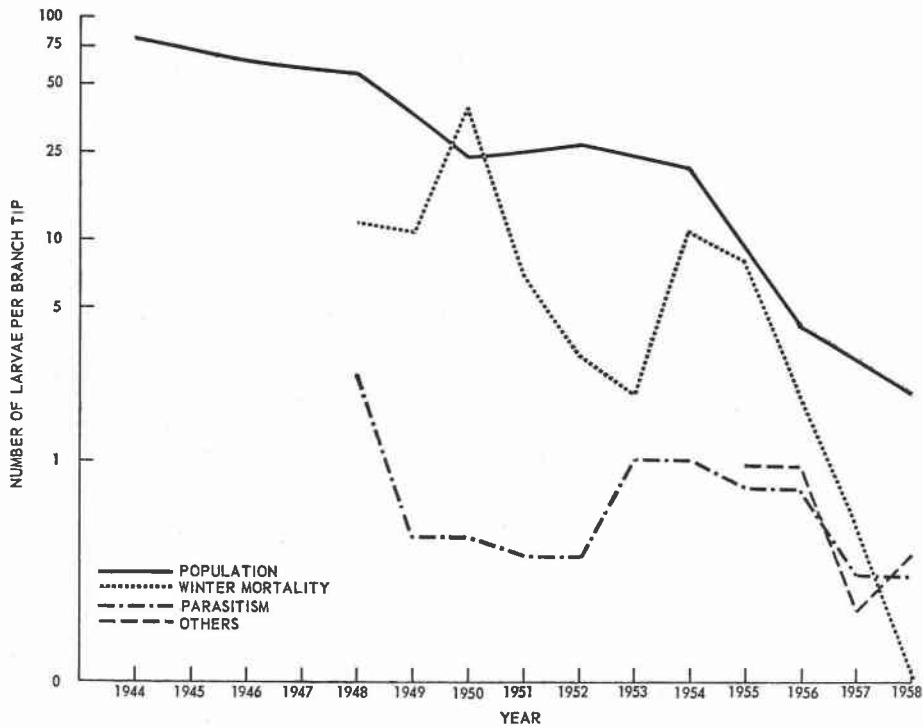


FIG. 9. Comparison of winter mortality, parasitism, and other mortality with respect to host population.

spent. Thalenhorst (46) has presented several European examples of insect outbreaks attributed to weather conditions. From observational evidence he shows that weather may influence an insect population in many ways: acting directly on the population, by its effect on some other factor which is fundamental to population growth (or lack of growth); by acting on the other factor and the population simultaneously with a reciprocal effect between population and factor; or by a maze of interactions involving soil, host-plant, population, and its enemies simultaneously, with interactions between the factors affected.

TABLE X

Per cent parasitism of lodgepole needle miner

Year	All averaged	Mt. Eisenhower, 5400 ft	Massive	Girouard	Cathedral
1944	3				
1946	3				
1948	10				
1950	13	15	—	11	—
1952	17	12	—	—	22
1954	14	16	10	16	14
1956	49	60	50	52	34
1958	46	41	47	54	40

The development of thought concerning weather in relation to insect outbreaks has slowly given more importance to weather as a causal agent. However, Wellington (56) has pointed out that although the literature is replete with papers dealing with the effects of various meteorological factors on many phases of insect development and behavior, only a few deal with those effects in terms of large scale weather processes and a very few follow through to the logical conclusion: prediction of biological phenomena with the aid of more modern methods of weather analysis and forecasting. Wellington (56) has developed probably the first inclusive theory relating insect abundance and weather which has been applied to three outbreak situations in Canada with considerable success (9, 55, 58):

"To assess climatic influences correctly it is necessary to examine climatic variations during the period immediately preceding or coinciding with the beginning of an outbreak of an insect that exhibits violent fluctuations in numbers instead of studying the climate while the outbreak exists. This follows from the concept of climatic release of a small indigenous population. That is, in a region where a species exists in small numbers, and in which biotic conditions already favour population growth no initial increase may occur until seasonal climatic control is relaxed. The important point to keep in mind however, is that favourable weather may have to recur several years in succession before a major increase in population can develop. Once the enormous potential for increase that such a species possesses is realized, the population grows so rapidly that no combination of adverse physical or biotic factors can halt it immediately. Since it is usually during this period that the outbreak is studied, it is not surprising that effects of the various original governing factors are often obscured."

In summary, the theory of climatic release explains the time and place of outbreaks and its worth may be measured by its ability to predict outbreaks. In its present stage of development, it does not explain the fluctuations in numbers in the manner of comprehensive theories. Studies on population dynamics in forest entomology during the periods of low numbers are rare,

although it is apparent that fluctuations in numbers without loss in "balance" are common and outbreaks the exception. Within the period of low numbers, increase in population from one year to the next can result from physical conditions becoming favorable to the insect. Readjustment of the population after this increase may come through density-related processes although these may not be entirely effective until physical conditions again become unfavorable. However, years with unfavorable weather conditions cannot always be expected to follow years with favorable conditions and eventually the favorable weather conditions occur several years in succession. During such a period, as the climatic theory postulates, the low populations may be released from the controlling influence of both physical and biotic factors (57).

#### THE THEORY OF CLIMATIC RELEASE APPLIED TO THE OUTBREAK OF THE LODGEPOLE NEEDLE MINER

A comparison of early weather records with those known to have caused a decline in needle miner populations showed that conditions which caused high mortality in needle miner populations occurred with relatively high frequency (Figs. 10 and 11). The longest interval between severe winters occurred from 1937 to 1950, the period during which the past needle miner outbreak occurred. The outbreak was discovered in 1942, confined to the middle altitudes. The fact that populations were found there and were increasing indicates that the outbreak was in a relatively early stage of development. Empirical calculations showed that the needle miner population could increase from a single pair per branch tip in 6 years (three generations) to numbers in excess of those found. If we assume one fertilized female per branch tip in the first year with an egg-laying capacity of eight eggs and a series of mild winters where total mortality did not exceed 20% in any one year, the population in the sixth year would be greater than 100 per tip. Thus, it is possible, beginning with the generation in 1938, that a comparable population growth to that postulated did occur owing to the series of mild winters following 1936-37. The assumption of one fertilized female per branch tip as an initial density is reasonable according to current samples (1958). The concentration of larvae per tip did not occur at the intermediate levels (elevations) probably because of dispersal throughout uninfested stands at other altitude levels and valley bottom (54). The severe winters commencing in 1945-46 undoubtedly reduced the populations to the lower densities of 1938 and earlier.

The needle miner outbreak studied was restricted to the valleys of Banff National Park and adjacent areas in Yoho and Kootenay parks. The failure of the needle miner to increase east of Banff Park may be explained on climatic grounds. The reasons for the failure to increase in the west are not so clear. The mean monthly temperatures at Edson, Rocky Mountain House, and Exshaw show that the eastern slopes of the Rocky Mountains are generally colder than the outbreak area. This is also demonstrated in the Climatological Atlas for Canada (47). This is because the cold cA air usually flows south across the prairies and then moves laterally into the outbreak area from an

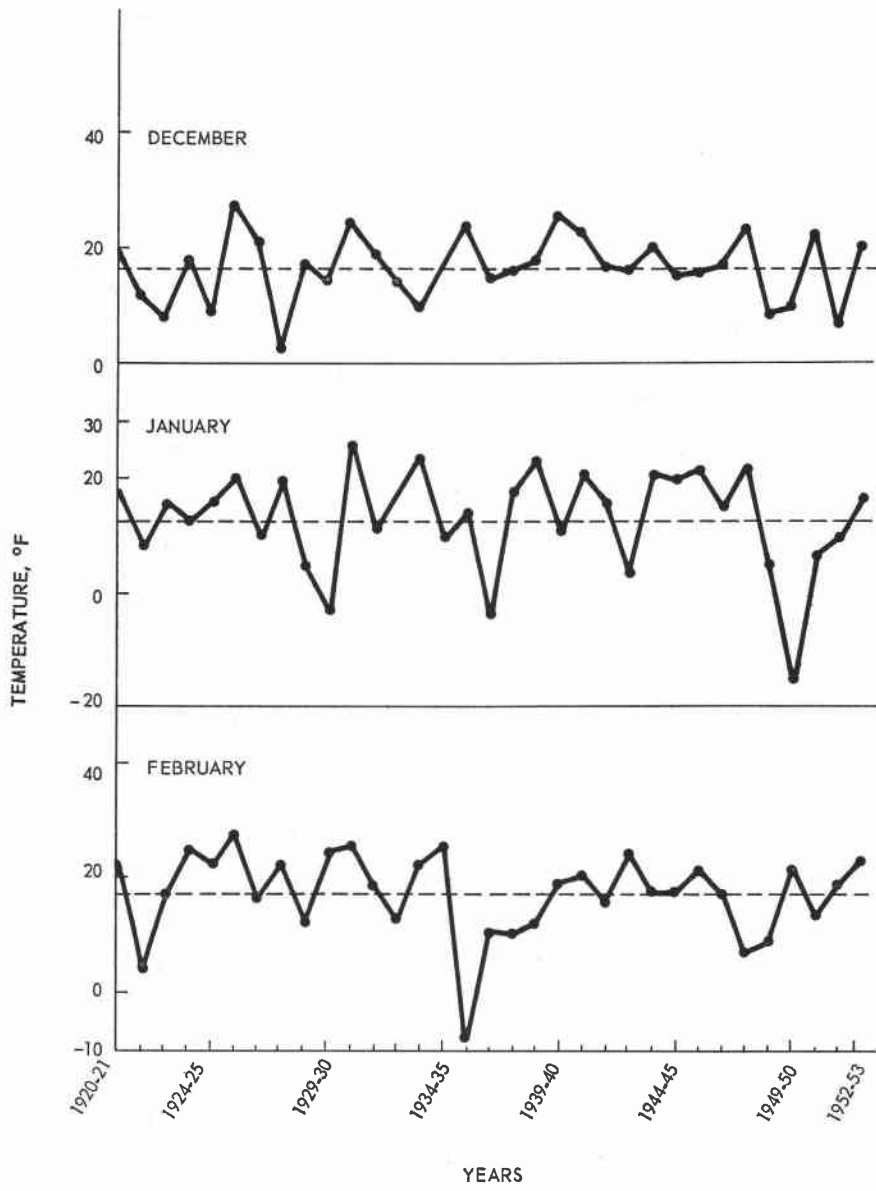


FIG. 10. Mean monthly temperatures 1920-21 to 1952-53 for Banff, Alberta.

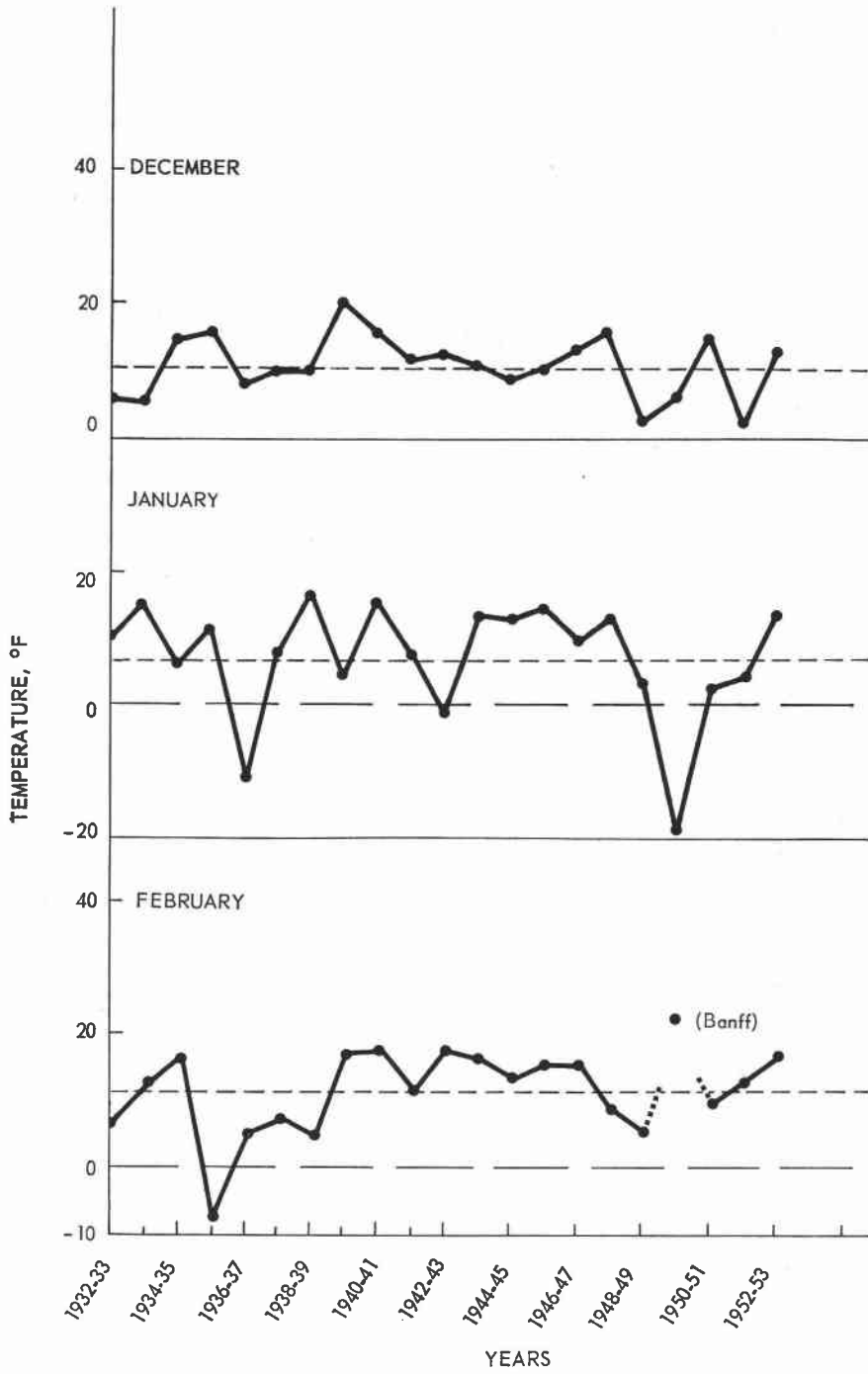


FIG. 11. Mean monthly temperatures 1932-33 to 1952-53 for Lake Louise, Alberta.



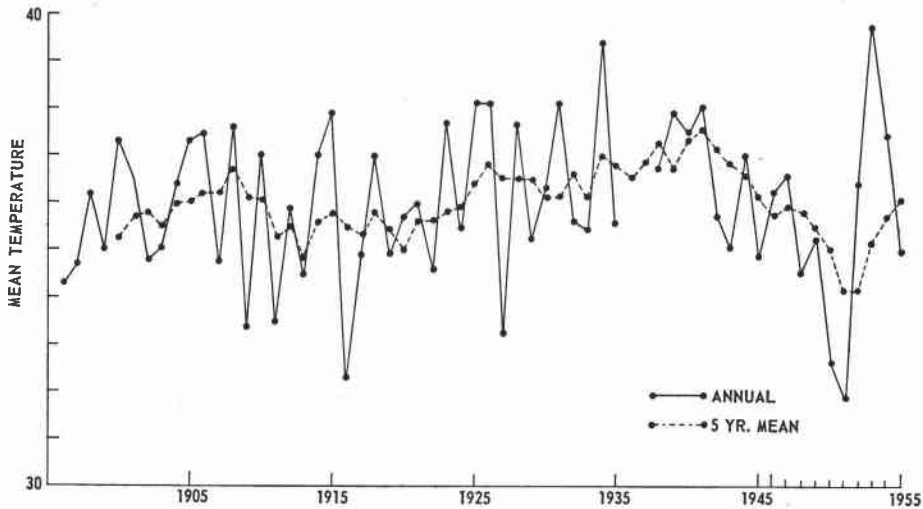


FIG. 12. Mean annual temperature and 5-year running average annual mean temperature for Banff, Alberta, 1896 to 1955.

easterly or northeasterly direction. The mountains frequently block or diminish this penetration into the valleys. Circulation in Yoho and Kootenay parks is more complex than that in Banff Park (11). Climatic fluctuations in these areas are often more violent than in Banff Park, even though the winter extremes may not be as severe. The failure of needle miner populations to increase west of Banff Park may be linked to violent fluctuations of climate acting upon stages other than larvae, rather than to sustained low temperatures, as in Banff Park.

Yearly average temperatures were calculated for Banff, Alberta, plotted as a 5-year running average (Fig. 12) (19). A definite warming period is shown from about 1925 to 1948. However, there were several years prior to 1936-37 when the winters were comparable to that of 1949-50; this supports the assumption that the outbreak began about 1938. Evidence of a real climatic change not attributable to random fluctuations has been compiled and it shows that the climate of northern regions of the world did become warmer about 1940 (56). From the weather records presented in the text and others available it is unlikely that an outbreak of comparable magnitude was able to occur prior to that time. Tree ring studies do not show any evidence of a previous outbreak (26, 43). It would follow from these observations that in this region the "normal" climate is too severe to permit the occurrence of sustained outbreaks of *Recurvaria starki* Free.

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### References

1. ALLEE, W. C., EMERSON, A. E., PARK, O., PARK, T., and SCHMIDT, K. P. Principles of animal ecology. W. B. Saunders Co., Philadelphia, Pa. 1949.
2. ANDREWARTHA, H. G. and BIRCH, L. C. The distribution and abundance of animals. Univ. Chicago Press, Chicago, Ill. 1954.
3. BATZER, H. O. and BENJAMIN, D. M. Cold temperature tolerance of the European pine shoot moth in lower Michigan. J. Econ. Entomol. **47**, 801-803 (1954).
4. BLAIS, J. R., PRENTICE, R. M., SIPPELL, W. L., and WALLACE, D. R. Effects of weather on the forest tent caterpillar, *Malacosoma disstria* Hbn., in central Canada in the spring of 1953. Can. Entomologist, **87**, 1-8 (1955).
5. BROWN, A. W. A. In Ann. Rept. Forest Insect Survey. Can. Dept. Agr., Div. Entomol., Sci. Serv., Ottawa. 1942.
6. DEBACH, P., FISHER, T. W., and LANDI, J. Some effects of meteorological factors on all stages of *Aphylis lingnanensis*, a parasite of California red scale. Ecology, **36**, 743-753 (1955).
7. FRANZ, J. Über die genetischen Grundlagen des Zusammenbruchs einer Massenvermehrung aus inneren Ursachen. Z. angew. Entomol. **31**, 228-260 (1949).
8. GRAHAM, K. and STARK, R. W. Lodgepole needle miner (bionomics). Can. Dept. Agr., Div. Entomol. Bi-Monthly Progr. Rept. **5**(6), 2 (1949).
9. GREENBANK, D. O. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm. I. The role of climate. Can. J. Zool. **34**, 453-476 (1956).
10. HARVILLE, J. P. Ecology and population dynamics of the California oak moth *Phryganidia californica* Packard (Lepidoptera:Dioptidae). Ph.D. Thesis, Stanford University, California. 1956.
11. HENSON, W. R., STARK, R. W., and WELLINGTON, W. G. Effects of the weather of the coldest month on winter mortality of the lodgepole needle miner, *Recurvaria* sp. in Banff National Park. Can. Entomologist, **86**, 13-19 (1954).
12. HODSON, A. C. An ecological study of the forest tent caterpillar, *Malacosoma disstria*. Hbn. in northern Minnesota. Univ. Minn. Agr. Expt. Sta. Tech. Bull. 148 (1941).
13. HOPPING, G. R. Lodgepole pine needle miner. Can. Dept. Agr., Div. Entomol. Bi-Monthly Progr. Rept. **2**(4), 3 (1946).
14. HOPPING, G. R. The lodgepole pine needle miner in western Canadian parks. Can. Dept. Agr., Div. Entomol. Proc. Publ. 59. Ottawa. 1946.
15. HOPPING, G. R. Rocky Mountain region. Can. Dept. Agr., Div. Entomol. Bi-Monthly Progr. Rept. **4**(4), 3 (1948).
16. HOPPING, G. R. Timber types in relation to insect outbreaks in the Canadian Rocky Mountains. 81st Ann. Rept. Entomol. Soc. Ontario, 72-75 (1950).
17. HUTCHINSON, R. N. Influence of winter night temperatures on the California red scale. J. Econ. Entomol. **40**, 921-922 (1947).
18. LEECH, H. B. In Ann. Rept. Forest Insect Survey—British Columbia and western Alberta. Can. Dept. Agr., Div. Entomol., Sci. Serv., Ottawa. 1944.
19. LONGLEY, R. W. Mean annual temperatures and running mean temperatures for selected Canadian stations. Can. Dept. Transport, Meteorol. Div., Circ. 2481. Tec. 186. 1954.
20. LORD, F. T. and MCPHEE, A. W. The influence of spray programs on the fauna of apple orchards in Nova Scotia. VI. Low temperatures and the natural control of the oystershell scale, *Lepidosophes ulmi* (L.) (Homoptera:Coccidae). Can. Entomologist, **85**, 282-291 (1953).
21. MCGUFFIN, W. C. In Annual report of the Forest Insect Survey. Can. Dept. Agr., Div. Entomol., Ottawa. 1948.
22. MCGUFFIN, W. C. Forest Insect Survey. Can. Dept. Agr., Div. Entomol. Bi-Monthly Progr. Rept. **5**(2), 3-4 (1949).
23. MILLS, H. B. Weather and climate. In U.S.D.A. yearbook, Insects. 1952.
24. MILNE, A. The natural control of insect populations. Can. Entomologist, **89**, 193-213 (1957).
25. MORGAN, F. D. Factors influencing the abundance of *Recurvaria milleri* Busck (Lepidoptera:Gelechiidae). Ph.D. Thesis, University of California, Berkeley, California. 1955.
26. MOTT, D. G., NAIRN, L. D., and COOK, J. A. Radial growth in forest trees and effects of insect defoliation. Forest Sci. **3**, 286-304 (1957).
27. NICHOLSON, A. J. The balance of animal populations. J. Anim. Ecol. **2**, 132-178 (1933).

28. NICHOLSON, A. J. Fluctuation of animal populations. Rept. Australian New Zealand Assoc. Advance. Sci. **26**, 134-148 (1947).
29. NICHOLSON, A. J. An outline of the dynamics of animal populations. Australian J. Zool. **2**, 9-65 (1955).
30. NOLTE, H. W. Beitrage zur Epidemiologie und Prognose des Rapserrdflohs (*Psylliodes chrysocephala* L.). Beitr. Entomol. (Berlin) **3**, 518-529 (1953).
31. PATTERSON, J. E. Life history of *Recurvaria milleri* Busck, the lodgepole needle miner in Yosemite National Park, California. J. Agr. Research, **21**, 127-142 (1921).
32. SALT, R. W. Influence of moisture content and temperature on cold-hardiness of hibernating insects. Can. J. Zool. **34**, 283-294 (1956).
33. SCHWERDTFEGER, F. Grundriss der Forstpathologie. Paul Parey, Berlin. 1950.
34. SHEPHERD, R. F. Lodgepole needle miner, *Recurvaria milleri* Busck. Can. Dept. Agr., Div. Entomol. Bi-Monthly Progr. Rept. 6(6), 3 (1950).
35. SOLOMON, M. E. The natural control of animal populations. J. Animal Ecol. **18**, 1-35 (1949).
36. SOLOMON, M. E. Dynamics of insect populations. In Ann. Rev. Entomol. **2**, 121-142 (1957). Palo Alto, Calif.
37. STARK, R. W. Lodgepole needle miner. Can. Dept. Agr., Div. Entomol. Bi-Monthly Progr. Rept. **5**(1), 3 (1949).
38. STARK, R. W. Analysis of a population sampling method for the lodgepole needle miner in Canadian Rocky Mountain Parks. Can. Entomologist, **84**, 316-321 (1952).
39. STARK, R. W. Distribution and life history of the lodgepole needle miner (*Recurvaria* sp.) (Lepidoptera: Gelechiidae) in Canadian Rocky Mountain Parks. Can. Entomologist, **86**, 1-12 (1954).
40. STARK, R. W. Life tables for the lodgepole needle miner, *Recurvaria starki* Free. (Lepidoptera: Gelechiidae). Proc. Xth Intern. Congr. Entomol. **4**, 151-162 (1958).
41. STARK, R. W. Population dynamics of the lodgepole needle miner, *Recurvaria starki* Free. (Lepidoptera: Gelechiidae) in Canadian Rocky Mountain Parks. Ph.D. Thesis, University of British Columbia, Vancouver, B.C. 1958.
42. STARK, R. W. Climate in relation to winter mortality of the lodgepole needle miner, *Recurvaria starki* Free. in Canadian Rocky Mountain Parks. Can. J. Zool. **37**, 753-761 (1959).
43. STARK, R. W. and COOK, J. A. The effects of defoliation by the lodgepole needle miner (*Recurvaria starki* Free.). Forest Sci. **3**, 376-396 (1957).
44. STEPHEN, W. P. and BIRD, R. D. The effect of barometric pressure upon oviposition of the imported cabbageworm, *Pieris rapae* (L.). Can. Entomologist, **81**, 132 (1949).
45. SWEETMAN, H. L. Successful examples of biological control of pest insects and plants. Bull. Entomol. Research, **26**, 373-377 (1935).
46. THALENHORST, W. Other aspects of population dynamics (in German). Twelfth Congress IUFRO 56/24/19. 1956.
47. THOMAS, M. K. Climatological atlas for Canada. Dept. Transport, Meteorol. Div., Div. Building Research, N.R.C. No. 3151(41), Ottawa. 1953.
48. THOMPSON, W. R. On natural control. Parasitology, **21**, 269-281 (1929).
49. THOMPSON, W. R. Biological control and the theories of the interactions of populations. Parasitology, **31**, 299-388 (1939).
50. THOMPSON, W. R. Theory of natural and biological control. In Ann. Rev. Entomol. **1**, 379-402 (1956). Palo Alto, Calif.
51. ULLYETT, G. C. Mortality factors in populations of *Plutella maculipennis* Curtis (Tineidae: Lepidoptera) and their relation to the problem of control. S. African Dept. Agr. Forest Entomol. Mem. **2**, 77-202 (1947).
52. UVAROV, B. P. Insects and climate. Trans. Entomol. Soc. London, **79**, 1-247 (1931).
53. WELLINGTON, W. G. Conditions governing the distribution of insects in the free atmosphere. I. Atmospheric pressure, temperature and humidity. Can. Entomologist, **77**, 7-15 (1945).
54. WELLINGTON, W. G. Conditions governing the distribution of insects in the free atmosphere. IV. Distributive processes of economic significance. Can. Entomologist, **77**, 69-74 (1945).
55. WELLINGTON, W. G. Air-mass climatology of Ontario north of Lake Huron and Lake Superior before outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.) and the forest tent caterpillar, *Malacosoma disstria* Hbn. (Lepidoptera: Tortricidae: Lasiocampidae). Can. J. Zool. **30**, 114-127 (1952).
56. WELLINGTON, W. G. Atmospheric circulation processes and insect ecology. Can. Entomologist, **86**, 312-333 (1954).
57. WELLINGTON, W. G. Weather and climate in forest entomology. Meteorol. Monogr. **2**, 11-18 (1954).
58. WELLINGTON, W. G., FETTES, J. J., TURNER, K. B., and BELYEA, R. M. Physical and biological indicators of the development of outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Can. J. Research, D, **28**, 308-331 (1950).