WEATHER AND LARCH SAWFLY SURVIVAL

by

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INTRODUCTION

The initiation or collapse of a forest insect infestation has often been attributed to various weather phenomena, and weather conditions are known to have a marked effect on the survival of the larch sawfly, Pristiphora erichsonii (Hartig). This insect spends about 10 months of its annual life cycle in a cocoon in the soil or duff beneath the trees, and most workers have concentrated their attention on the cocoon stage. In upland sites, and more rarely in bog sites, prolonged hot, dry weather can cause desiccation and death of the larvae in the cocoon (Graham 1931, Graham 1956, Graham and Satterlund 1959). In bog sites, excess moisture can cause severe mortality during the cocoon stage, either by drowning the insects in the flooded cocoons (Lejeune, Fell and Burbidge 1955, Graham 1956, Graham and Satterlund 1959, Drooz 1960) or by creating adverse moisture conditions in the cocoon environment (Ives and Nairn 1966). Flooding for short periods in August or early September caused almost complete mortality and adult emergence from cocoons immediately above this maximum water table was greatly reduced, even though the cocoons were never inundated.

The effects of weather on the active stages of the insect are usually more difficult to assess. Larvae dropping to spin cocoons may drown in surface pools; if this surface flooding coincides with peak larval drop the amount of mortality can be appreciable (Ruggles 1910, Butcher 1951, Ives 1968). Wind and rain have also been observed to dislodge feeding larvae (Hewitt 1912, Britton 1915, Graham 1956) and most of the immature larvae among them probably died before reaching foliage (Ives 1963). Temperatures of 40°C or more, even for brief periods, are fatal for sawfly adults (Graham 1956) and larvae (Heron 1967). Usually, both adults and feeding larvae

are able to avoid these excessively high temperatures, but there are exceptions reported in the literature. Fyles (1907) reported numbers of sawfly adults dying after alighting on the extremely hot deck of a ferry. Ruggles (1911) stated that in 1910, a hot, dry year in Minnesota, 'the larch sawfly did not remain on the tamarack as long as they had in previous years, leaving while the trees still showed green. Also, the cocoons were considerably smaller than they had been in previous years.' This statement can be interpreted as meaning that the larvae dropped prematurely in 1910, possibly because of defoliation and high temperatures. Drooz (1960) reported a similar condition in Minnesota in 1952, and he noticed that larvae attempting to crawl up the trunks of trees 'were killed and baked hard on the tree trunks'. Ives (1967) also reported premature larval drop in 1961, a hot, dry year in Manitoba, that could not be attributed to food shortages, as population levels were low at the time.

The foregoing references provide ample evidence that weather conditions do in fact affect larch sawfly survival, but they do not provide any quantitative relationships between weather conditions and survival. This report gives the maximum bark surface temperature in various parts of tamarack crowns in 1967, and relates some of these to other more easily obtained measurements. It also examines other meteorological and biological data collected by the Forest Research Laboratory, Winnipeg, to determine whether or not there are any predictable relationships between gross weather measurements and larch sawfly mortality during the adult, egg and feeding larvae stages.

TEMPERATURES IN TAMARACK CROWNS.

Temperatures in the crowns of tamarack near the Forestry Research Field Station on Red Rock Lake, Manitoba, were measured with copperconstantan thermocouples connected to a recording potentiometer. Six thermocouple junctions were placed in firm contact with the bark on twigs of last year's growth, about 1/8 inch in diameter, six on twigs about 1/4 inch in diameter, another six on the trunks, and two were shielded to measure the ambient air temperatures in the tree crowns. A 24-point recording potentiometer, operating on a 30 second printing cycle, was used for recording the temperatures; readings for each thermocouple were therefore recorded every 12 minutes.

In addition, a thermograph, a recording pyranometer and a cup-type gust recording anemometer were operated in a swamp about a mile away.

These instruments were part of the meteorological station operated in conjunction with each of several larch sawfly study plots.

Seasonal Trends

The daily maximum surface temperatures on the 1/8 and 1/4 inch twigs were considerably higher than the maximum ambient air temperatures, except on very cloudy days (Figs. 1 and 2). Temperatures on the 1/8 inch twigs were commonly 5 or 6 degrees higher than the ambient air temperature, while those on the 1/4 inch twigs differed by almost twice this amount. Temperatures of exposed bark on the trunks (not shown) equalled or exceeded those on the 1/4 inch twigs, but were not always adequately assessed because of shade cast by the foliage. During the period 19 June to 16 August, the temperatures on the 1/4 inch twigs reached or exceeded 37°C, the lowest temperature that Heron (1967) found to be lethal for last-instar larch sawfly larvae, on a total of 21 days, but the surface of the 1/8 inch twigs reached these temperatures on four occasions only.

Daily Trends

Daily temperature courses for six of the hottest days show that the lowest temperatures occurred at 0500 to 0600 hours, after which they rose rapidly unless there was cloud cover (Figs. 3-8). The surface temperatures on exposed 1/4 inch or larger twigs or on the trunks often remained above 37°C for several hours, although they soon dropped to near air temperature whenever the surface was shaded. The trunks cooled off more slowly, and remained a few degrees above air temperature for several hours. The surface temperatures on the 1/8 inch twigs seldom reached 37°C, and then only for very brief periods.

INDIRECT ESTIMATION OF MAXIMUM BARK TEMPERATURES

The direct measurement of bark surface temperatures is not practical except on a limited basis. Indirect methods for estimating maximum bark temperatures were therefore attempted, as outlined in the following paragraphs.

The data in Figs. 1 and 2 suggest that radiation and possibly wind speed might be of some use in estimating the temperature increase, relative to ambient air temperature, on the 1/8 inch and 1/4 inch twigs. However, the results (Figs. 9-12) indicate that wind speed was of no use whatever for predictive purposes, and sky radiation wasn't much better. The correlations of .563 and .651 between radiation and temperature increases on 1/8 inch and 1/4 inch twigs were almost entirely due to radiation readings of 0.70 cal cm⁻² min⁻¹ or less; if these values were removed the correlations become insignificant. Radiation readings are useful, however, for indicating cloudy or partly cloudy days.

The ambient air temperatures, eliminating cloudy and partly cloudy days as indicated by radiation readings, provide the best indirect estimate of maximum bark surface temperatures on the 1/8 inch and 1/4 inch twigs.

Temperatures on the 1/8 inch twigs would probably not reach 40°C unless the ambient air temperature reached 35°C (Fig. 13), suggested by Graham (1956) as a temperature that might force larvae to drop from the trees prematurely. In Manitoba, air temperatures seldom reach this level. The highest air temperature recorded between 19 June and 16 August 1967 was 33.5°C on 20 July. Temperatures on the 1/4 inch twigs, however, reached 40°C when the ambient air temperature reached 30°C, and this temperature was reached several times during the same period (Fig. 14).

Measurements of the crown air temperatures in the trees were available for this study only. A comparison was therefore made between crown air temperatures and the trunk space air temperatures recorded in a Stevenson screen about 1 mile away (Fig. 15). The correlation between the two temperatures was excellent; the crown air temperatures were higher than the trunk space air temperatures by about 2°C at 20°C and by about 3°C at 30°C. Therefore, possibly lethal temperatures of 40°C or more can be expected on exposed 1/4 inch twigs whenever the thermograph readings exceeded 28°C, and on exposed 1/8 inch twigs whenever the readings exceeded 32°C. Whether or not these temperatures cause lethal effects depends upon the extent to which the insects avoid exposure to them.

LARCH SAWFLY MORTALITY

The following sections examine data on larch sawfly mortality to determine if there are any predictable relationships with weather conditions.

Adult Mortality

The mortality of adult larch sawfly was assessed by the numbers of eggs laid per female, rather than the length of time that each individual lived, because a female that laid 50 eggs in two days and then died is just as effective in propagating her species as one that lived for two weeks before laying the same number of eggs. The numbers of eggs per female were obtained by caging females on tamarack in the field. In 1959, 1 to 5-day old adults were placed individually in small wire and cloth sleeve cages tied to branch tips bearing at least three new shoots. Prior to caging in the field, the sawfly adults were held in an insectary in well ventilated cages containing wads of absorbent cotton soaked in a solution containing sugar and water. Only large, apparently vigorous females were used. In 1961 and 1962 groups of six adults in the same age classes, and held under similar conditions in an insectary, were placed in large 6-ft³ dacron marquisette cages enclosing small tamarack trees. The numbers of eggs laid were determined after the adults had died.

The mean numbers of eggs per female in 1959 showed some relationship to the age of the females when placed on the trees; the younger ones laid more eggs (Table I). However, the large cages used in 1961 and 1962 required more adults than emerged in one day, so it was necessary to hold them in an insectary until enough were obtained. The 1959 data were therefore pooled. Unfortunately, the use of mixed age classes probably increased variability, which was already high, and this may have masked differences in oviposition rates related to weather. The small sleeve cages seemed to raise the internal

temperature several degrees, depending upon the amount of shading, and even the large cages raised the temperature slightly. For this reason the number of eggs per adult were not plotted against temperature, but are shown chronologically (Fig. 16).

The mean numbers of eggs per female were generally higher in 1959 than in 1961 or 1962, although the large cages should have provided more favorable conditions. The apparent decrease in variability is merely a reflection of the grouping of six adults in each cage. There is no evidence of any significant seasonal pattern. The lowest mean rate of oviposition, for 1961 and 1962 adults, occurred among those put in cages on June 26, 1961, and June 25-26, 1962. The 4-day periods following these dates were the hottest for period shown, 31.5°C in 1961 and 30°C in 1962, but it is difficult to determine if this coincidence has any biological significance.

Egg and Early Larval Mortality

Mortality during the egg and early larval stages was determined by collecting shoots bearing oviposition scars and the associated colonies of larvae (Ives 1962) from several plots during the period 1957-1966. Data were not used unless a total of at least 100 egg scars were obtained at each collection point on each date; first-and second-instar collections were pooled, as experience has shown that there is very little mortality between the first and second instars. The percentage mortality shows no relationship to date of collection (Fig.17).

The data in Fig. 17 were collected from several plots during an eight year period. Variation between plots and years might therefore mask any seasonal trends, so mortality was plotted against the maximum air temperature in each plot during the four days preceding the date of collection, and against the average hour-degrees above 50°F for each plot during the week preceding the date of collection. Neither of these expressions reduced the amount of scatter, so it must be concluded that temperature has no predictable effect on egg and early larvae survival.

This lack of predictability may be due to variation in the exposure of individual colonies. In 1961, small potted tamarack were caged with female sawfly in a shaded location until oviposition occurred. Half of the trees were then placed on a platform in full sun, while the others were placed on the same platform in 95% shade. A maximum-minimum mercury thermometer was placed in a ventilated shelter in the shaded enclosure and checked daily. After hatching was complete, all larvae were removed and counted, and the number of egg scars determined. Survival on the exposed trees was appreciably less than on the shaded ones in four of the eight trials (Table II). These differences may have been due to high temperatures. The results also seem to indicate that the larch sawfly is most vulnerable to high temperatures during the late egg or early firstinstar larval stages. The insects in trials 1 and 2 were both exposed to the same maximum temperature, 33°C, but mortality was higher in trial 1 than in trial 2. Similarly, the insects in trials 4, 5 and 8 were exposed to the same maximum temperature of 31.5°C; those in trials 4 and 8 were adversely affected while those in trial 5 were not. Abortive feeding notches made by larvae that failed to become established were further evidence that a critical period for survival occurred immediately following eclosion. In trials 5 and 7 the survival was greatest on the exposed trees; occasional light rain was falling during the periods of hatching, and the dense shade may have slowed foliage drying sufficiently to cause increased mortality.

It is unlikely that egg clusters under natural conditions are subjected to the dense shade used in the above experiment. A limited number of first—and second-instar larvae from exposed and shaded locations were therefore collected in 1967 to determine if natural shading had any effect on egg and early larval survival (Table III). Survival among the exposed colonies was less than among the shaded ones. The reason for this difference is not clear. The maximum air temperature during the 4 days preceding the date of collection was 33°C for the sample collected on 21 July, and adverse temperature conditions in the exposed locations could have caused increased mortality. However, the corresponding temperature for the first two collections was only 27°C, yet the difference between survival in shaded and exposed locations was 18.8% for the the collection made on 3 July and 8.8% for the collection made on 10 July. Temperature is therefore probably not the only component of weather affecting larch sawfly egg survival.

Late-instar Larvae Mortality

The percentage of larvae dropping prematurely from the trees into oil traps changed at weekly intervals (Ives 1967) was used as an indication of late-instar larvae mortality during the period 1965-1967. Premature larvae drop included the third, fourth and early fifth instars. For the purpose of

this report only apparently healthy larvae were used, and any first-or second-instar larvae caught have been disregarded because of the small numbers involved and the unreliability in detecting them among the frass and other litter accumulated in the traps. Data from three plots, near Pine Falls, Riverton and Hodgson, were not included because the dwarfing caused by a recently introduced parasite, Olesicampe (Holocremnus) sp. nr. nematorum Tschek (Muldrew 1967) could not easily be separated from premature larval drop.

A number of factors may contribute to premature larval drop. The more obvious are wind, rain, heat and lack of food. Meteorological instruments were operated in each plot to obtain records for the first three, while weekly defoliation estimates for the trees above the traps provided some indication of the lack of food. Experience has shown that ocular estimates of the percentage defoliation are extremely unreliable, especially when a number of individuals are making the estimates over a period of time. A numerical rating of defoliation, ranging from 0 to 100, was therefore devised, based upon a number of defoliation categories (Table IV). Although more complex than percentage defoliation estimates, it is probably more reliable.

The weekly defoliation rating for each tree was determined, and those in the same class were pooled. If less than 50 larvae dropped from trees in any particular defoliation category the data were either discarded or pooled with adjacent defoliation categories. A mistake in procedure occurred in 1967, and each week's data had to be pooled and an average defoliation rating used: fortunately, the range in defoliation rating for each week was not too large.

Premature larval drop was plotted against defoliation rating, maximum rainfall per 10-minute period, maximum gust velocity and maximum air temperature (Figs. 18-21). The amount of scatter is large in each of the four graphs; consequently it is difficult to assess visually the relative importance of these four expressions in relation to the percentage of premature drop. The data were therefore subjected to stepwise multiple regression analyses to determine which expression showed any relationship (Snedecor 1956). As Snedecor points out, these tests are not independent, but the results (Table V) indicate that defoliation rating and wind gust velocity are significantly related to premature drop. The points in Fig. 20 suggest that a single observation at 55 mph may contribute most to this significance. When the set of data containing this observation is removed from the analyses the F value for gust velocity is much smaller, although it is still significant at the .05 level (Table VI).

The relationship between premature larval drop (Y), defoliation rating (X₁) and maximum wind gust velocity (\mathbf{X}_2) is expressed by the formula: $\mathbf{Y} = -28.65 + 0.34\mathbf{X}_1 + 0.99\mathbf{X}_2$. This equation was used to calculate expected percentages of premature larval drop for various defoliation ratings and wind gust velocities (Table VII). These values are tentative; additional data are required on premature larval drop at high wind gust velocities.

DISCUSSION

egg and feeding larval stages is difficult to assess under field conditions. Adults and feeding larvae will die when exposed to temperatures of 40°C or more for brief periods under experimental conditions. The bark surface on exposed trunks and branches often exceeds this temperature, but the insects are often able to avoid those extremes; the adults by burrowing into moist moss, the larvae by hanging vertically on the foliage to avoid some of the radiant heating. Changing patterns of light and shadow also limit the exposure of a large part of the population. The insects may also be more vulnerable to high temperatures at certain stages in the life cycle. Well developed embryos and newly-hatched larvae seem to be more susceptible to heat than are newly-laid eggs or older larvae.

Prolonged periods of light rains may adversely affect the survival of the delicate newly-hatched larvae, but will have very little effect on the survival of eggs or older larvae. Heavy rains may dislodge some larvae; the numbers dislodged will be variable, due to differences in the amount and severity of exposure and amount of defoliation. Graham (1956) reported that larvae were dislodged from one side of the trees but not the other.

Wind may be the one facet of weather that has a demonstrable effect on late-instar larval survival, perhaps due in part to the whipping action of the trees in strong winds, which may affect a larger proportion of the larvae present than either rain or radiant heating. Variability remains large, however, and it is doubtful if equations using wind velocity have much predictive value.

This report has been largely unsuccessful in relating larch sawfly monthly to various weather phenomena. This failure may be due to lack of adequate measurements of weather conditions, although more sophisticated instrumentation is impractical. It may also be due to incorrect usage of available weather data; it is conceivable that other expressions might yield better results. Detailed studies of the insect's behavioral responses to the wide range of weather conditions occurring in nature might help to clarify the relationships between the various components of weather and larch sawfly survival. In the author's opinion, however, the most probable explanation for the apparent lack of relationships lies in the high degree of variability in exposure to the various hazards. If this is so, it is unlikely that refinements in techniques will improve the relationships appreciably. It is therefore concluded that weather conditions will have very little value in the preparation of descriptive or predictive models for the population dynamics of the larch sawfly.

ACKNOWLEDGEMENT

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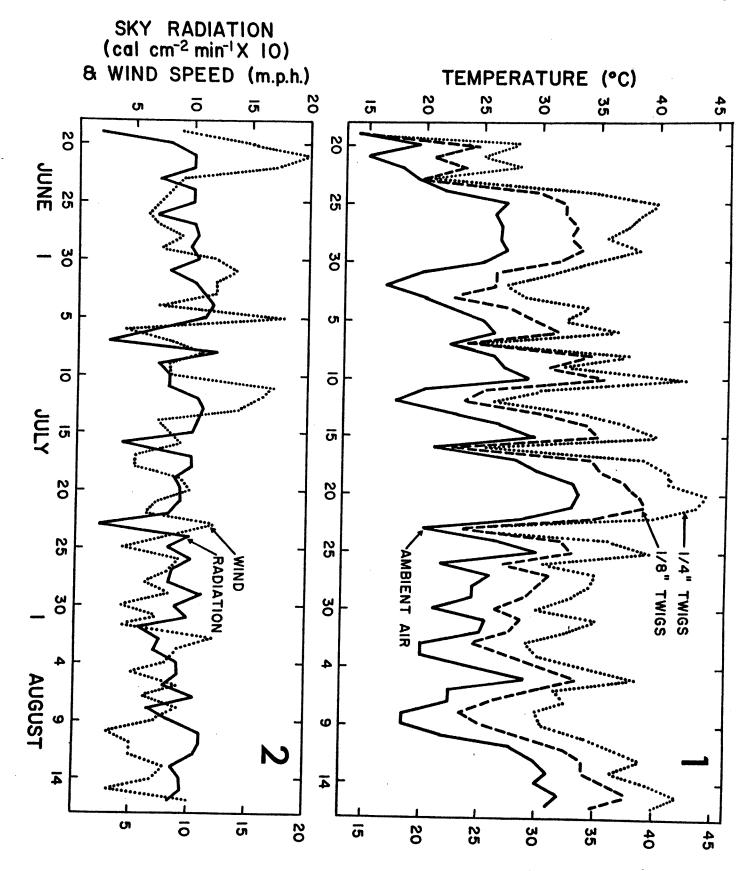
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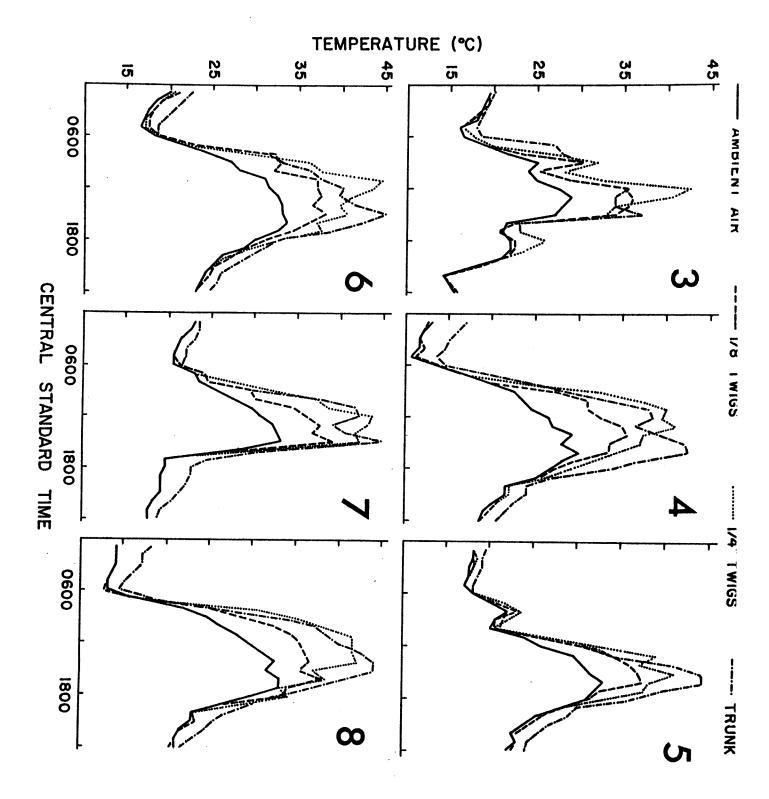
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- Figs. 1-2. Temperature, wind and radiation measurements recorded from 19 June to 16 August 1967 at Red Rock Lake, Manitoba.
 - Daily maximum bark surface temperatures on 1/8
 inch and 1/4 inch twigs and maximum ambient air
 temperatures.
 - 2) Daily mean gust velocities from 1000 to 1600 hrs. CST and daily mean cal cm⁻²min⁻¹ from 0800 to 1400 hrs.



Figs. 3-8. Maximum air and bark surface temperatures during each hour for selected days. 3) July 10.

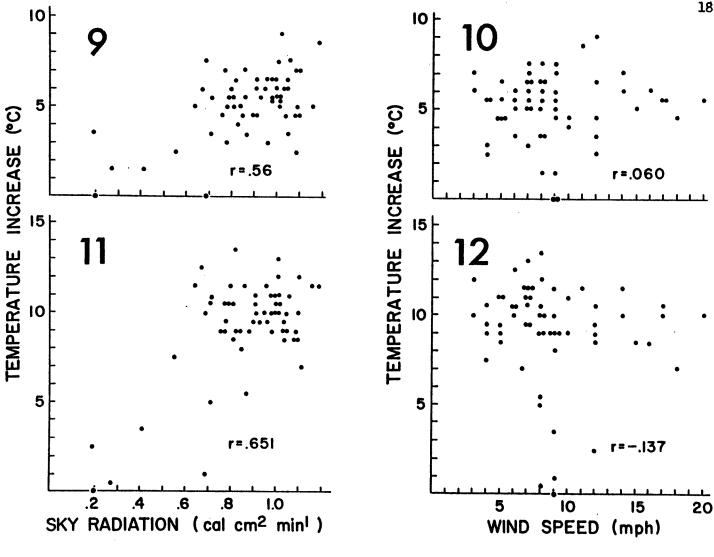
- 4) July 18. 5) July 19. 6) July 20.
- 7) July 21. 8) August 15.

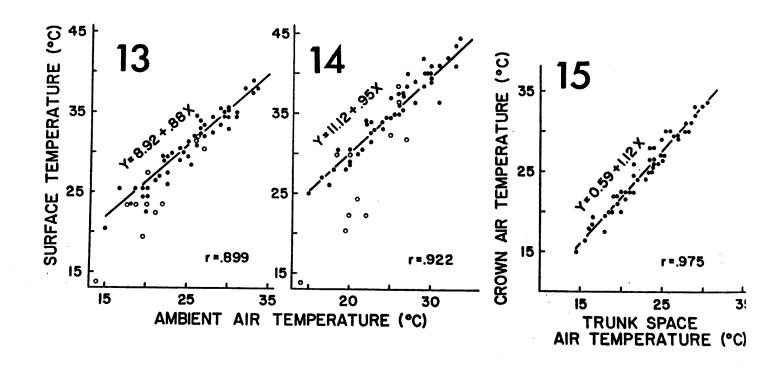


Figs. 9-15. Temperature relationships. 9-12. Temperature increases in relation to sky radiation and wind speed.

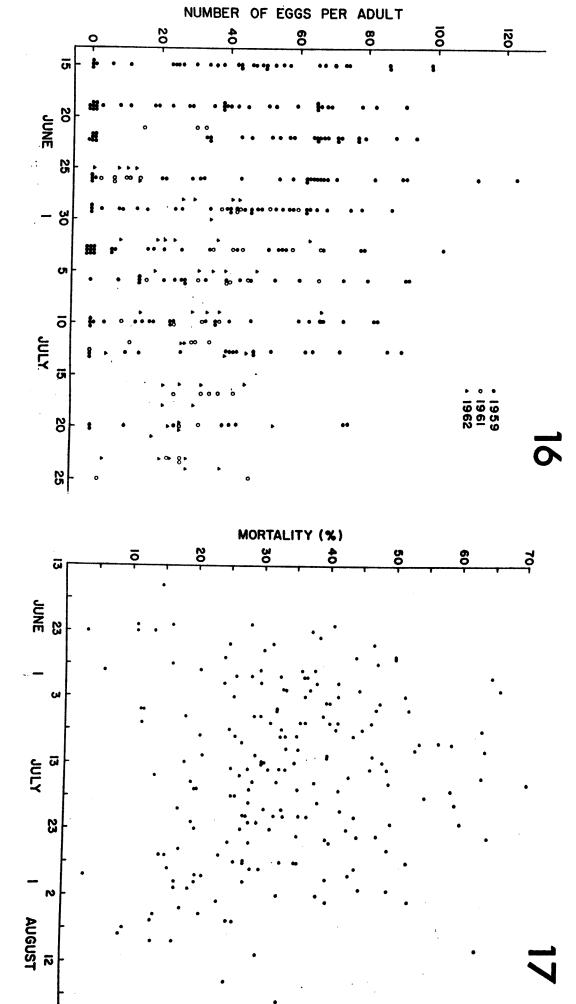
9 and 10) On 1/8-inch twigs. 11 and 12) On 1/4-inch twigs. 13-14. Surface temperature in relation to ambient air temperature. Open circles represent cloudy or partly cloudy days and were not used in calculating regressions or correlation coefficients. 13) on 1/8-inch twigs. 14) On 1/4-inch twigs. 15. Crown air temperature in relation to trunk space air temperature.



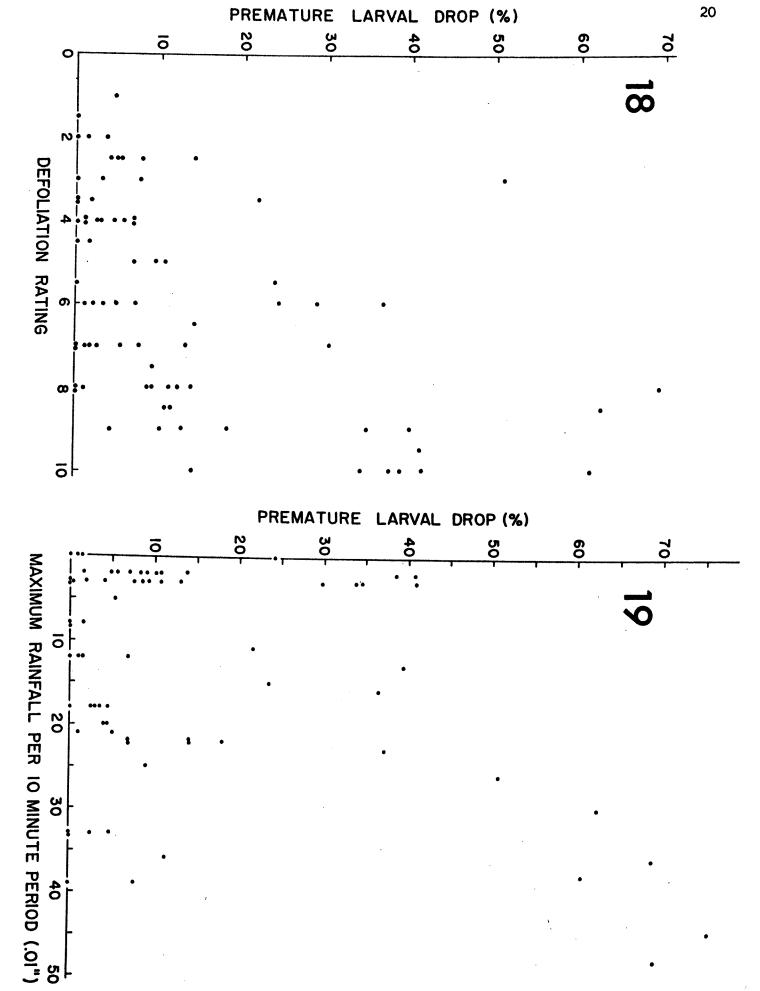












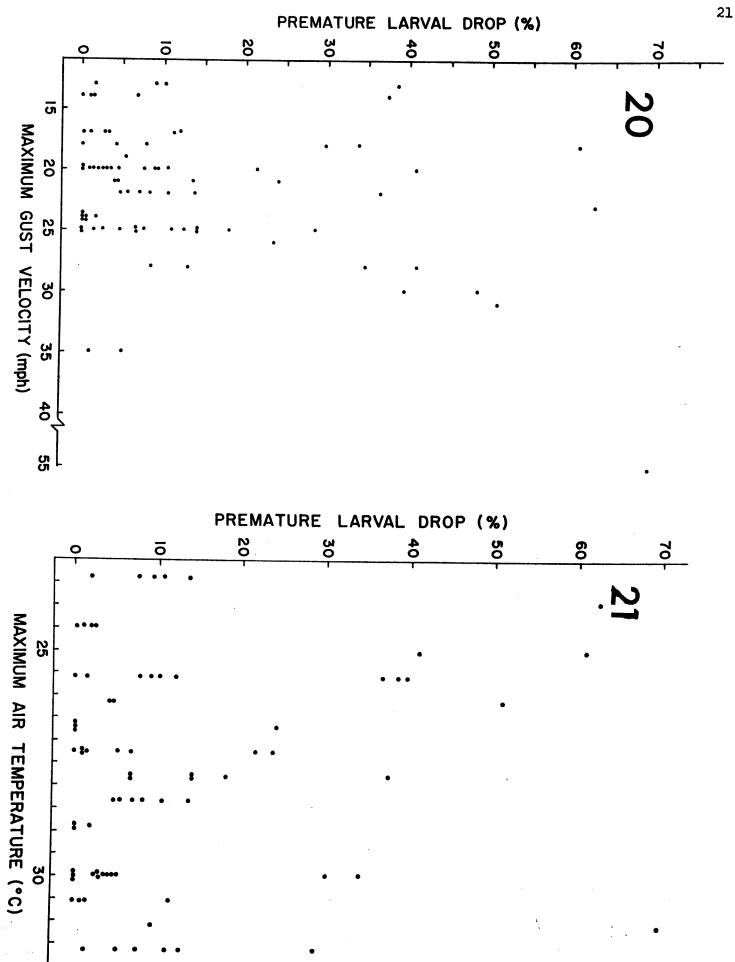


TABLE I

Seasonal distribution in the mean numbers of eggs deposited by female larch sawfly of different ages when caged on tamarack in 1959 (Numbers of adults in parentheses)

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Date		<u>ì</u>	2	3	44	5	
June	15	55(5 <u>)</u>	55(5)	47(5)	56(5)	22(5)	
	19	41(5)	48(4)	49(5)	13(4)	27(4)	
	22	82(2)	53(5)	55(6)	52(5)	43(3)	
	26	84(5)	38(5)	64(1)	34(4)	61(5)	
	29	71(2)	34(4)	50(5)	33(5)	58(4)	
July	3	69(3)	24(5)	43(4)	67(1)	•	
	6	40(4)	27(3)	42(5)	41(5)	-	
	10	100	55(3)	36(5)	29(3)	42(4)	
	13	43(2)	57(4)	13(2)	-	-	
	20	56(2)	-	-	52(3)	11(3)	

TABLE II

Effect of artificial shading on egg and early larval survival of larch sawfly
in 1961

Trial	Dates of tests (inclusive)	No.	•	No.	shaded	Maximum ter	
IIIaI	(TUCTUSTA6)	eggs	survival	eggs s	survival	Date	<u> </u>
1	June 22 - July 1	359	17.0	479	63.9	June 28	92
2	June 26 - July 2	686	49.3	358	73.7	June 28	92
3	June 30 - July 6	285	56.1	318	56.9	July 6	86
4	July 3 - July 11	585	74.5	635	84.6	July 9	89
5	July 7 - July 13	583	85.9	747	76.3	July 9	89
6	July 10 - July 18	439	82.9	545	83.9	July 17	81
7	July 14 - July 20	404	88.1	331	71.0	July 19	85
8	July 18 - July 25	421	70.5	456	88.88	July 25	89

TABLE III

Effect of natural shading on egg and early larval survival of larch sawfly
in 1967

Date Collected	Expose No. Eggs	ed <u>Location</u> **Survival	Shaded Location No. % Eggs Survival
July 3	180	57.8	231 76.6
July 10	223	61.0	106 69.8
July 21	181	77.3	163 90.8

TABLE IV

Numerical ratings assigned to various categories of larch sawfly defoliation

of tamarack

		Lower 2/3 of crown					
Upper 1/3 o	f crown		ch ti	p s	Whole br	anches	
		Nil	Few	Numerous	Several	Numerous	Complete
	Nil	0	10	20	-	•	•
Branch tips	Few	10	20	30	40	400	-
	Numerous	20	30	40	50	60	80
	Several	30	40	50	60	70	90
Whole Branches	Numerous	cia-	50	60	70	80	100
	Complete	œ	60	70	80	90	100

TABLE V Multiple regression analyses of relationships between percentage premature drop of larch sawfly larvae (Y) and defoliation rating (X_1) , maximum air

temperature (X_2) , maximum gust velocity (X_3) and maximum rainfall intensity (X_4) .

Sources of variation	Degrees of freedom	Sums of squares	Mean squares	F Values
Regression on X_1 and X_2	2	4914.72		
Regression on X ₁ alone	1	4648.88		
X ₂ after X ₁	1	265.84	265.84	1.26
Regression on X_1 and X_2	2	4914.72		
Regression on X ₂ alone	1	274.48		
X_1 after X_2	1.	4640.24	4640.24	21.96
Error	67	14155.87	211.28	
Regression on X1, X2, and X3	3	8251.14		
Regression on X and X2	2	4914.72		
X_3 after X_1 and X_2	1	3336.42	3336.42	20.35
Error	66	10819.45	163.93	
Regression on X1, X2, X3 and	X ₄ 4	8465.52		
Regression on X_1 , X_2 and X_3	3	8251.14		
X_4 after X_1 , X_2 and X_3		214.38	214.38	1.31
Error	65	10605.07	163,15	

Multiple regression analyses of variates as in TABLE V, with set of data containing highest gust velocity omitted

	Degrees	Sums		
Sources of montation	of	of	Mean	F
Sources of variation	freedom	squares	squares	Values
Regression on X_1 and X_2	2	4586.32		
Regression on X ₁ alone	1	3973.19		
X ₂ after X ₁	1	613.13	613.13	3.57
Regression on X_1 and X_2	2	4586.32		
Regression on X ₂ alone	1	667.16		
X ₁ after X ₂	1	3909.16	3909.16	22.74
Error	66	11346.48	171.91	
Regression on X_1 , X_2 and X_3	3	5535.25		
Regression on X1 and X2	2	4586.32		
X_3 after X_1 and X_2	1	948.93	948.93	5.93
Error	65 /	10397.55	159.96	
Regression on X ₁ , X ₂ , X ₃ and X ₄	4	5695.94		
Regression on X_1 , X_2 , and X_3	3	5535.25		
X_4 after X_1 , X_2 and X_3	1	160.69	160.69	1.00
Error	64	10236.86	159.95	

TABLE VII

Predicted percentages of premature larval drop for various combinations of defoliation ratings and maximum gust velocities

Defoliation		Maximum wind gust velocities (mph)							
ratings	15	25	35	45					
10	0	0	9	19					
20	0	3	13	23					
30	0	6	16	26					
40	0	10	20	30					
50	3	13	23	33					
60	7	17	27	36					
70	10	20	30	40					
80	14	24	33	43					
90	17	27	<i>3</i> 7	47					
100	20	30	40	50					