PHYTOSOCIOLOGICAL AND ENVIRONMENTAL CHARACTERISTICS OF OUTBREAK AND NON-OUTBREAK AREAS OF THE TWO-YEAR CYCLE SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA*[1]

R. F. SHEPHERD
Forest Zoology Laboratory, Calgary, Alberta

INTRODUCTION

In the most severe outbreak areas in the eastern and western parts of North America, the spruce budworm, *Choristoneura fumiferana* (Clem.) (Tortricidae), maintains a one-year life cycle. Within the Canadian Rocky Mountains, however, the budworm's life cycle lasts two years. The outbreaks are also quite different in character. The two-year cycle budworm is present in most of the spruce-fir stands of this region, but high populations recur only in certain restricted stands within this spruce-fir forest. This would indicate that there are essential habitat differences between the outbreak and non-outbreak areas which affect the ability of the budworm to reproduce and survive. Detailed descriptions were made of the soil, plant, and climatic characteristics of these two habitats from a forest community viewpoint. Differences in the environmental conditions between the habitats led to an evaluation of the factors affecting the favorable development of the budworm. The importance of these factors was investigated by assessing budworm survival under the two sets of environmental conditions.

The study areas were located in Banff, Yoho, and Kootenay National Parks in the Canadian Rocky Mountains. Eight outbreak areas were located from past records, and seven non-outbreak

[1] Contribution No. 484, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada; based on a thesis submitted to the Graduate School of the University of Minnesota in partial fulfillment of the degree of Master of Science, June 1955.

areas were selected by the presence of the budworm in suitable host stands where no outbreaks had been reported. These study areas were homogeneous stands of at least four acres. Four of the areas were selected for intensive studies.

The terms "outbreak" and "non-outbreak" are relative, depending upon population levels between two areas. The budworm can usually be found in either outbreak or non-outbreak areas, but the populations in the former are consistently higher than those in the latter, even in years of generally low abundance. When the macroclimate is favorable for budworm increase, the populations rise in all areas, but much more so in the outbreak areas. During the highest observed populations, the trees in outbreak areas are noticeably defoliated and red tops are quite conspicuous. In the non-outbreak areas many new shoots are defoliated and the budworm is quite common, but extensive defoliation of trees does not take place.

Assistance is gratefully acknowledged to Messrs. B. McPhee, J. K. Robins, A. E. Anderson, and E. F. Thornton for their help in setting up equipment and collecting data; Miss M. Cumming kindly undertook the detection of larval diseases; Mr. D. I. Crossley, formerly of the Canadian Forestry Branch, helped in the soil analysis; and Dr. A. E. Porsild of the Canadian National Museum checked the plant identifications. Special thanks are due to Dr. A. C. Hodson, Dept. of Entomology and Economic Zoology, University of Minnesota, Mr. G. R. Hopping, Officer-in-Charge of the Calgary Forest Zoology Laboratory, and other research officers for advice in the study and for a critical review of the paper.

Life History of the Two-Year Cycle Budworm

The two-year cycle budworm feeds on old and new foliage of Engelmann spruce (*Picea engelmanni* Parry) and alpine fir (*Abies lasiocarpa* (Hook) Nutt.), preferring the new needles of developing buds. A single brood predominates; most adults occur during the even-numbered years with few or none during the odd-numbered years. Greatest defoliation is by late-instar larvae in the even-numbered years. Defoliation in odd-numbered years is usually light enough so that the trees have a chance to recover.

Mathers (1932) first determined the life history of the two-year cycle spruce budworm in British Columbia. This work was repeated by Cook (1953) in the Rocky Mountain area. The eggs are laid towards the end of July and hatch in approximately two weeks. The young larvae do not feed, but spin hibernacula, moult, and overwinter in the second stadium. The next year they feed throughout June as second- and third-instar larvae. Each larva spins a second hibernaculum the first week in July, then moults and overwinters as a fourth-instar larvae. They feed throughout June of the second year as fourth, fifth, and sixth instars and pupate the first week of July. The moths emerge two weeks later.

Forest Type and Density

The spruce-fir stands of this region are mature to overmature climax types, at the end of a sere initiated by fire. Lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) usually follows the fire, and after one to three hundred years the pine is replaced by Engelmann spruce. Shortly after the spruce becomes the dominant tree, alpine fir enters and soon dominates the understory. The large spruce in the overstory are capable of good steady growth for 300 years (Le Barron and Jemison 1953), and often persist for another 150 years before dying. Usually a few remnant lodgpole pine are also present in this upper layer. The fir seldom lives beyond 150 years, but it is capable of seeding and establishing greater numbers of seedlings than the spruce.

Studies in the one-year cycle areas indicated that the danger of stands being damaged by the spruce budworm was related to age and volume of balsam fir, *Abies balsamea* (L.) Mill. (Westveld 1945, Balch 1946). This relationship between forest type and budworm outbreaks was investigated in the two-year cycle area by cruising a half-acre plot in each of the two outbreak and two non-outbreak areas. All trees over one inch DBH were recorded by species and diameter; all trees under one inch DBH were recorded by species and height. Crown cover was estimated using the line intercept method of Lindsey (1955). One thousand feet of transect were laid out and the intercepts of all crowns above breast height were recorded.

A summary of the stand statistics appears in Table I. There is no consistent difference in stand density, or in forest composition as expressed by percentage of fir present. The difference in basal area between outbreak and non-outbreak areas is a result of differences in site factors. A discussion of site will follow later. There is a striking difference in total crown area between outbreak and non-outbreak areas. The former have an average of 59 per cent of the area open, while the latter have 41 per cent of the area open.

Difference in crown cover is important to the

TABLE I. Summary of stand statistics

Plot Number	OUTBREAK		NON-OUTBREAK	
	I	II	III	IV
Basal area/sq. ft./acre	148	133	213	201
No. trees/acre	757	478	1028	608
Per cent fir	81	66	80	62
Per cent crown cover of total area				
—spruce	20	18	35	32
—fir	18	5	24	22
—other (including dead trees)	6	14	1	4
—open	56	63	40	42

ecoclimate of the stand. The more open a stand, the greater the air movement and penetration of radiation and thus the higher the evaporation rates. As will be shown later, this difference in crown cover, through its effect on the ecoclimate, is important to vegetation and to budworm populations.

SITES AND SOILS

Workers in the one-year cycle areas found no relationship between site quality and susceptibility of stands to budworm outbreaks (Jaynes and Speers 1949, Turner 1952). Conversely, the data collected on basal and crown areas indicated that site quality is important in the two-year area. The height and age of ten dominant and co-dominant spruce were measured in each of eight outbreak and seven non-outbreak areas. The ages of ten spruce saplings 4.5 ft. in height from each of the four study plots were used to convert age at breast height to total age. The site indexes were determined by extrapolation to height at 100 years from yield tables for Engelmann spruce (Anonymous 1947). The mean site index and standard error were calculated for each plot and are listed in Table II. They fall into two distinct groups according to outbreak and non-outbreak areas with the non-outbreak areas having considerably higher site indexes.

Soil samples were collected from each horizon. These were air dried and stored in cellophane bags until autumn when the texture and acidity of each sample were determined. For the pH readings the soils were screened, mixed with distilled water, and allowed to stand for twenty-four hours. Three determinations were made with a Beckman pH meter and averaged. Soil moistures *in situ* were determined with Fiberglass Soil Moisture Units and an ohmmeter. Calibration curves were established in the laboratory from sample cores according to standard procedure (Coleman 1950).

Most of the soils are immature. Those of the poorer sites (outbreak areas) are considerably more podzolized with a thin, ash-colored, typical A_2 layer and a conspicuous, red-brown illuvial layer. The duff layer is thin, acidic, and intermeshed with mycelial strands. The soils of the non-outbreak areas are less acidic, with no obvious A_2 layer, but with traces of an A_1 layer. The duff layer, although still a mor, is close to a duff-mull. The substrates of the two areas show no consistent differences; they are usually of silt, sand, fine gravel, or glacial till.

TABLE II. Site index of each plot

Plot No.	OUTBREAK AREAS		Plot No.	NON-OUTBREAK AREAS	
	Mean Site Index (ht. in feet at 100 years)	Standard Error		Mean Site Index (ht. in feet at 100 years)	Standard Error
I	64	2.3	III	88	3.3
II	66	3.3	IV	93	2.5
V	59	1.7	VII	92	3.1
VI	74	2.4	X	90	2.7
VIII	66	1.9	XI	74	2.4
IX	56	2.8	XIII	104	5.3
XII	67	2.5	XIV	99	3.6
XV	57	2.8			
Average	63.6		Average	91.4	

There was considerable seasonal variation in the moisture contents of the soils at the 6-inch level, but at the 30-inch level they were relatively consistent. Approximate values were obtained of the wilting coefficient and field capacity of the soils at the 30-inch depth from Figure 34 of Lutz and Chandler (1946). In the outbreak areas the moisture contents were all close to the wilting coefficient so that moisture was probably limiting at certain periods during the summer. In the non-outbreak areas the percentage of soil moisture was consistently higher than field capacity, resulting in abundant moisture for plant growth at all times.

The studies of site index, soil profiles, and soil moisture all show evidence of a relationship between outbreaks and the site conditions, and indicate that outbreaks are restricted to the drier, poorer sites.

DESCRIPTIONS OF FOREST ASSOCIATIONS

Site differences are often expressed by the plant communities present. Each community develops only under certain habitat conditions, which include all the environmental factors influencing organisms living there. Over a long period of time most of the organisms of the region will, by chance, be given an opportunity to enter the community and, through competition, many of these are eliminated. Thus, by the time climax forests have evolved, the communities which have developed under similar habitat conditions will be

almost identical. Descriptions were made of the plant communities in the eight outbreak and seven non-outbreak areas to obtain an indication of their habitats.

The qualitative system of analysis proposed by Braun-Blanquet (1932) was used. The basis of his concept is the forest association which he believes is the fundamental unit of vegetation. Each association is made up of separate stands containing similar combinations of species. The basic distinction between the associations is made through use of fidelity of species for specific associations. That is, the presence of species in only one (predominantly in one) association is used to distinguish between associations. If the plants listed by Braun-Blanquet's system are supplemented with a list of the constant and dominant species, as suggested by Poore (1956), a good vegetative description is obtained.

Estimates were made of the abundance and phytosociological relationships of each species with the aid of scale values. Three characteristics of each plant were estimated: abundance (scale values 0-5), sociability (scale values 1-5), and vitality (scale values 1-4). From these, two other characteristics were derived: constancy (scale values 1-5), and fidelity (scale values 1-5). Representatives of each plant were collected and sent to the National Museum of Canada for confirmation or revision of field identification.

The areas fell into two distinct associations corresponding to outbreak and non-outbreak areas. This would indicate that the habitat conditions, as typified by one association, are conducive to periodically increasing budworm populations, while the conditions in the other association are not.

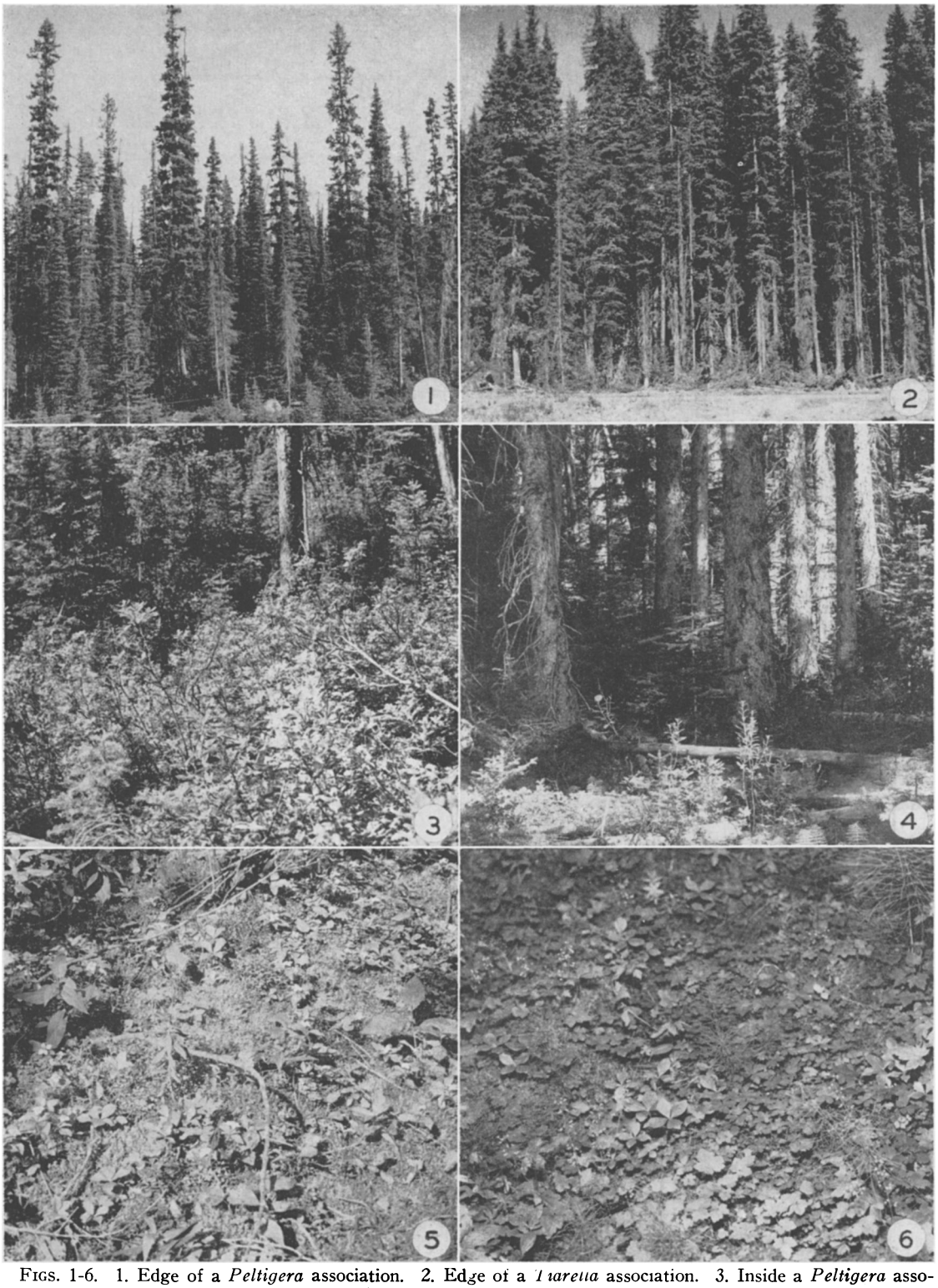
The name proposed for the association which occurs in outbreak areas is *Picea engelmanni-Abies/Peltigera aphthosa* and that for the non-outbreak areas is *Picea engelmanni-Abies/Tiarella unifoliata*. Figures 1 to 6 are comparative photographs of these associations.

The *Peltigera* association occurs on dry sites, usually on steep slopes of the mountains, where drainage is good, the water table deep, and exposure to radiation and drying winds great. The soil is a definite podzol with an acid mor humus and a thin A^2 layer. The red-brown illuvial layers are also quite acidic, and the texture varies from silt to clay loam.

The trees of the overstory are mature to overmature Engelmann spruce with a few residual lodgepole pine and some older alpine fir. The crown conditions are poor; much of the foliage is covered with bearded lichens and shoot growth

TABLE III. Plants of highest indicator value listed by fidelity. Figures refer to average estimates based upon scale values

		Constancy	Abundance	Vitality
	Picea engelmanni—Abies/Peltigera apthosa Association (Outbreak Type)			
Fidelity 5	Exclusive Species			
	None			
Fidelity 4	Selective Species			
	Cladonia gracilis Willd.	3	0.6	3.0
	Ledum glandulosum Nutt.	2	1.5	2.5
	Elymus innovatus Beal.	2	1.5	1.5
Fidelity 3	Preferential Species			
	Peltigera aphthosa Willd.	5	1.3	2.0
	Arnica cordifolia Hook.	5	1.3	2.3
	Menziesia ferruginea Smith var. *glabella* (Gray)	4	3.5	3.1
	Alectoria fremontii Tuck.	3	3.2	4.0
	Dicranum sp. near *scoparium* Hedw.	3	3.0	2.2
	Shepherdia canadensis (L.) Nutt.	3	1.4	3.0
	Juniperus communis L. var. *sibirica* Ait.	3	0.7	2.5
	Pyrola secunda L.	3	0.6	2.7
	Usnea sp.	3	low	2.0
	Empetrum nigrum L.	2	1.0	3.0
	Cladonia sylvatica Hoffm.	1	1.0	2.0
	Picea Engelmanni—Abies/Tiarella unifoliata Association (Non-outbreak Type)			
Fidelity 5	Exclusive Species			
	Tiarella unifoliata Hook.	4	1.6	3.2
	Rubus pedatus Smith	4	2.1	3.6
	Streptopus amplexifolius (L.) D.C.	4	1.0	3.2
	Equisetum arvense L.	3	3.0	3.5
	Galium triflorum Michx.	3	1.7	3.5
	Dryopteris disjuncta (Ledeb.) C.V. Mort.	3	1.2	2.2
	Petasites palmatus (Ait.) Gray	3	1.0	3.5
	Smilacina racemosa (L.) Desf.	3	low	2.7
Fidelity 4	Selective Species			
	Ribes lacustre (Pers.) Poir.	5	0.8	2.7
	Rubus pubescens Raf.	3	1.3	2.3
	Mitella nuda L.	3	1.0	3.5
	Amelanchier alnifolia Nutt.	3	1.0	1.0
	Clintonia uniflora (Schult.) Kunth.	3	0.6	3.5
	Mnium sp. near *venustum* Mitt.	2	1.0	3.0
	Osmorhiza obtusa (C. & R.) Fern.	1	1.0	4.0
Fidelity 3	Preferential Species			
	Hypnum crista—castrensis Hedw.	5	2.5	3.5
	Lonicera involucrata (Richards.) Banks.	4	1.0	2.5
	Rosa sp.	4	low	0.8
	Thalictrum occidentale A. Gray	3	1.7	3.0
	Vaccinium membranaceum Dougl.	3	1.7	2.7
	Rubus parviflorus Nutt.	3	1.3	2.7
	Scopania sp. near *Blonderi* Aust.	3	0.7	3.5
	Fragaria glauca (S. Wats.) Rydb.	3	0.7	1.2
	Pyrola virens Schweigger	3	low	2.5
	Acer Glabrum Torr. var. *Douglasii* (Hook) Dipp.	3	low	1.3
	Lonicera utahensis Wats.	1	1.0	3.0
	Salix sp.	1	low	1.0



FIGS. 1-6. 1. Edge of a *Peltigera* association. 2. Edge of a *Tiarella* association. 3. Inside a *Peltigera* association. 4. Inside a *Tiarella* association. 5. Typical *Peltigera* association. 6. Typical *Tiarella* association.

is slow with many buds remaining undeveloped. The narrow, ragged crowns provide little protection for the vegetation underneath. The heavy shrub layer is dominated by *Menziesia ferruginea*, but *Shepherdia canadensis* and *Juniperus communis* are also common. The ground is nearly

covered by herbs, mosses, liverworts, and lichens. As can be seen in Table III, none of the plants occur exclusively in the *Peltigera* association, and thereforefore no one species is a good indicator. Instead, a combination of plants dominated by *Menziesia* forms a characteristic group which typifies the association.

The association is similar to the one Daubenmire called *Picea engelmanni-Abies/Menziesia ferruginea* in Northern Idaho (1952). The most characteristic shrub is *Menziesia* in both associations. However, the lower herb and moss layers are completely different. In the *Menziesia* association of Idaho the lower layers are quite sparse with only a few species present, and much of the ground is either bare or covered by a thin layer of duff. In contrast to this, the ground of the *Peltigera* association is almost completely covered by plants.

The *Picea engelmanni-Abies/Tiarella unifoliata* association usually occurs in valley bottoms or on wet slopes where there is a high, dependable water table. Exposure is not extreme and the evaporation is comparatively low, so that the drying of the duff layer is not excessive. The soils are not podsolized to the same extent as in the *Peltigera* association. The duff layer is between a mor and a duff-mull, but still acidic. There are traces of an A_1 horizon, but usually the A_2 horizon is absent. The B horizons are slightly acidic and silty loam in texture.

The same species of trees are present as in the *Peltigera* association, but the crowns are full and vigorous. As a result, the protective value of the overstory is much greater. The shrub layer is not so extensive as in the *Peltigera* association; it is made of scattered shrubs of many species. The herb and moss layers contain many species which have a high indicator value such as *Tiarella unifoliata*.

This association is similar to the *Picea engelmanni-Abies/Pachystima Myrsinites* association of Daubenmire (1952). Differences in the shrub, herb, and moss layers separate the two; the most noticeable of these is the deep moist moss layer covering nearly all the area in the *Tiarella* association as compared with a much smaller area of mosses in the *Pachystima* association.

Forest Association Ecoclimates

Forest associations, such as the two described earlier, are the result of differences in the environmental factors. These same factors also affect the animal population and, through their changing influence on mortality and natality rates, may lead to fluctuations of the populations. As climate is one of the most variable of the environmental factors, it probably is a major cause of population fluctuations. The ecoclimates of the two associations were studied with emphasis placed on the factors which would most likely affect the budworm populations.

Evaporation was measured by means of circular copper pans 12 inches in diameter and 6 inches deep, with center posts. At each reading, water was added until the meniscus broke over the point of the central peg. The amount of water added was assumed to equal the evaporation since the last reading. The pans were set 36 inches from the ground; a roof was built above the pans to protect them from radiational heating and rain. Periodic cleaning prevented the accumulation of salts and debris on the surface. Drinking of water by birds was discounted because of the low bird population in the region.

Standard rain gauges were placed 12 inches above the ground in stand openings 20 to 30 feet wide; evaporation and precipitation readings were taken twice weekly. The rainfall showed no consistent differences between outbreak and non-outbreak areas. Hygrothermographs were set up in weather cabinets at standard height in plots I, II, and IV in 1952, in all four plots in 1953, and in plots II and IV in 1954.

The studies described above showed that soil moisture was more abundant in non-outbreak than in outbreak areas. Hygrothermograph charts showed that humidity during the afternoon period was generally lower in outbreak than in non-outbreak areas. The poor protective canopy in the outbreak areas permitted penetration of wind and sunshine. The combined effect of these factors resulted in greater evaporation in the outbreak areas. The evaporation over a four-day period when the weather was clear and sunny, was 0.110 cu. in per sq. in. of surface per day in outbreak areas, and 0.068 in. in non-outbreak areas. In contrast, when the weather was overcast and rainy, there was an evaporation of only 0.021 cu. in. in the outbreak areas and 0.020 cu. in. in the non-outbreak areas.

The total evaporation for the periods of larval activity for the three years of study is given in Table IV. For comparative purposes in this and the next study, the length of the period of larval activity is assumed to be constant (45 days), even though this may have varied somewhat between years and areas. The beginning of the period varied considerably between years, and this has been taken into account in the calculations. Considera-

ble differences in the evaporation rates between the two forest associations are indicated by the data.

TABLE IV. Evaporation during the periods of larval activity of 1952, 1953, and 1954

Plot No.	Total for period in.^{3}/in.^{2} of surface	Average for plots in outbreak or non-outbreak in.^{3}/in.^{2} of surface	% difference* between areas
1952			
I	2.95		
outbreak		3.15	
II	3.35		
			79
III	1.72		
non-outbreak		1.76	
IV	1.80		
1953			
I	2.60		
outbreak		2.69	
II	2.79		
			59
III	1.61		
non-outbreak		1.69	
IV	1.78		
1954			
II outbreak	4.34		
			95
IV non-outbreak	2.73		

* $\frac{\text{outbreak}-\text{non-outbreak} \times 100}{\text{non-outbreak}}$

As will be brought out later, the difference in evaporation may also influence budworm populations since survival seems to be greatest in the areas with the highest evaporation rates. This relationship between budworm populations and evaporation is based upon work carried out when populations were low. The relationship has been further tested by reconstructing the evaporation rates in the two associations prior to the last budworm outbreak. Precipitation at four local weather stations has been studied; also the annual frequency of cyclonic centers passing over the region has been calculated. These show a decrease in storm centers and precipitation in the period leading to the outbreak. However, such an analysis is too broad to enable close correlation with the type of small local populations that occurred in the two-year cycle areas.

Evaporation is affected by many factors, notably temperature, vapor pressure, wind, and radiation. These factors are interrelated, e.g., during fair weather there are usually high temperatures, low humidity, low winds, and a large amount of radiation. Records of one therefore, are often good indicators of the others. Only a few of these factors are available in the long term weather records, and of these it was believed that maximum temperatures would give the highest correlation to evaporation rates. An attempt was made to determine whether a correlation existed between maximum temperatures and evaporation rates collected from two summers' records in two outbreak and two non-outbreak areas. The evaporation measurements were made twice weekly and this represented the average evaporation for three- or four-day periods. The hygrothermograph charts were checked carefully to select periods when the weather was fairly uniform over these three- or four-day periods and average daily evaporation rates and average maximum temperatures were calculated. The data for the two plots were averaged yielding one set of data for each area. The correlation between the maximum temperatures and the rates of evaporation proved to be exceptionally good in both cases.

The evaporation rates of these areas were then correlated with the maximum temperatures of the closest weather station at Banff, approximately 25 air miles from the study areas. The regression curves are presented in Fig. 7. The regression equations are:

Outbreak area: $\log y + 1 = -0.10564 + 0.00203 x$ $(r = 0.956)$

Non-outbreak area: $\log y + 1 = 0.05368 + 0.00106 x$ $(r = 0.925)$

where y is the daily evaporation rate and x is the maximum temperature.

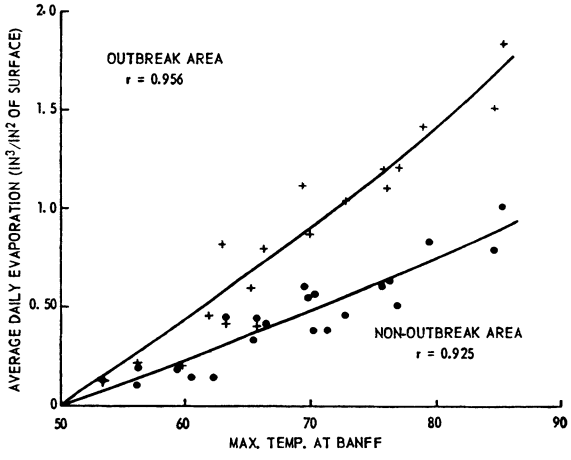


FIG. 7. Regression curve of the average daily evaporation rates in outbreak and non-outbreak areas in Kootenay National Park and the maximum temperature at Banff. Each point represents daily averages based on three- or four-day periods.

Such curves facilitate quick calculation of the evaporation rate from the maximum temperatures which occur in Banff. As these curves were based on average figures, it was still questionable if they would be accurate on a daily basis. The expected evaporation from the curves was com-

pared with the actual evaporation measured on the plots over the 127-day period, May 28 to September 30, 1952. Only half the points (11 representing 38 days) used to establish the curves came from this check period. The calculated evaporation was 2.9 per cent high for outbreak areas, and 1.2 per cent low for non-outbreak areas. As these were within acceptable limits of error, it was concluded that such results should allow the calculation, with a high degree of confidence, of evaporation rates in the study areas for the previous 25 years.

Evaporation was considered to be of major importance during the period of larval activity. The beginning of this period varies considerably from year to year (as much as four weeks). Rose and Blais (1954) showed that abundant larval emergence from overwintering hibernacula took place after maximum temperatures reached 60°F or above. The starting date for the present study was calculated by summing the degree days above 60° F from May 1 to the date of emergence during the years of study. It was found that larval activity began after about 60 degree days. This technique gives only a rough approximation of the commencement of larval activity, but permits better timing of the period for calculating the evaporation rates.

Evaporation rates for the outbreak and non-outbreak areas were estimated from 1928 to 1953 from Banff maximum temperatures. Records were not available for 1946 and 1948 and temperatures from Lake Louise were substituted. New regressions were not calculated for this station so evaporation estimates for these two years are approximate. The evaporation rates of every second year are plotted in Fig. 8, each point representing the period when the larvae of each generation feed openly upon the foliage and are most exposed to the influence of the weather.

Based upon the period 1948 to 1954, it was concluded that evaporation rates above 3.0 cu. in./sq. in. of surface for the last 45 days of larval activity are favorable for budworm increase. Starting in 1934, there were five successive generations of budworm which experienced these high evaporation rates. By the fifth generation, in 1942, budworm populations reached their climax and defoliated large areas of spruce-fir stands. In 1944, populations decreased and defoliation was less obvious. From 1948 to 1950, budworm populations in some restricted areas again increased to a point where defoliation was noticeable, and this increase was again associated with higher evaporation rates. Following 1952, populations declined.

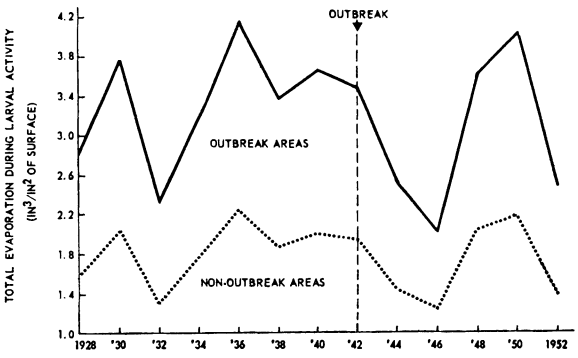


FIG. 8. The evaporation history of outbreak and non-outbreak areas for the period of larval activity, based upon Banff maximum temperatures. Only the even numbered years are plotted, as these are the years when the larvae are more exposed to weather influences.

This indicates that there is a correlation between the rates of evaporation and the fluctuations of budworm populations. In outbreak and non-outbreak areas, populations increased in years of high evaporation and decreased in years of low evaporation. Evaporation rates in the non-outbreak areas never approached the magnitude of the rates in the outbreak areas, and populations never reached a level high enough to cause noticeable defoliation.

Periodicity of Alpine Fir Flowering

The one-year cycle budworm feeds on staminate flowers as well as foliage of balsam fir. Staminate trees provide better food (Blais 1952), a favorable place to live (Wellington 1950a), and a preferred oviposition site (Blais, *op. cit.*). Thus, staminate trees commonly have more and faster developing larvae on them than non-staminate trees. Staminate flowers of alpine fir probably offer the same benefits to the two-year cycle budworm, and differences in this food factor between areas could account for the differences in budworm populations between outbreak and non-outbreak areas.

The relative abundance of staminate flowers over the past twenty years was determined from the flower scars on the branches. Twenty alpine fir trees in an outbreak area and twenty in a non-outbreak area were felled in 1953. The trees were largely co-dominants and were selected as probably supporting the greatest flower production by their size, crown quality, and exposure. From each tree, ten branches which were at least twenty years old were taken from the upper crown. The internodes of each branch were dated by counting back from the terminal bud and the presence or absence of staminate cone scars noted

The variation in flowering during the last twenty years in each area illustrated in Fig. 9. The

abscissa has been shifted one year to show the year of flowering instead of the year in which the buds were formed and upon which internode the resulting scars appeared. In the areas studied, defoliation was first noted in 1940 and became the heaviest in 1942. During the pre-outbreak period in this area, there was a steady increase in the amount of flowering up to the peak year of 1941.

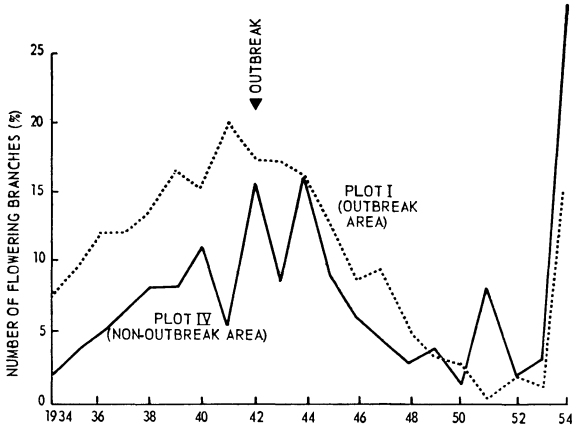


FIG. 9. Graph of the number of branches of alpine fir which bore flowers for each year from 1934 to 1954. The abscissa has been shifted one year to show the year of flowering instead of the year in which the buds were formed and upon which internode the resulting scars appeared.

In the non-outbreak area there was a similar increase up to 1940, but a severe reduction in 1941, the non-flight year previous to heavy defoliation. Nearly twice the flower production occurred in the outbreak areas as in non-outbreak areas.

Although the increase in the amount of flowering of alpine fir before the last outbreak may have aided the rise of budworm populations, the synchronization between areas suggests that the rise in flowering and in budworm populations may be the result of independent responses of both tree and insects to another factor, such as weather, rather than to a dependent relationship between the two. The study of the evaporation in the two forest associations indicates that there was a hot, dry period during the years of increased flowering. An increase in flowering following dry, sunny periods has been cited by a number of investigators. Morris (1948) found that the normal cycle of flower production of balsam fir (*Abies balsamea* (L.) Mill.) is interrupted by additional crops following hot, dry years.

VARIABILITY OF SEASONAL DEVELOPMENT

During the growing season frosts frequently occur in some parts of the region. As seasonal development may differ between outbreak and non-break areas, significant differences in larval mortality from late frosts, or in the co-ordination of larval emergence and foliage production, may appear which could give rise to different population levels between areas. Prebble (1945, 1948) noted a reduction in budworm populations due to frost in the Sault Ste. Marie district. He concluded that the amount of larval mortality was dependent on the time of spring emergence; mortality was greater in years when seasonal development started early in the year.

Differences in the rate of development may also be important to populations in outbreak and non-outbreak areas. Greenbank (1956) found that in years of favorable weather the budworm was able to feed upon early foliage and produced females with greater fecundity. In addition, shorter developmental time reduced the time of exposure to mortality factors.

The length and diameter of terminal shoots on five alpine fir and five Engelmann spruce saplings (3-5 ft.) were measured twice weekly in each of two outbreak and two non-outbreak areas during 1952. The radial increment of five dominant or co-dominant alpine fir trees on each plot were measured at breast height with a dendrometer. When dominant or co-dominant fir was not available, intermediate trees were used.

Collections of larvae were made every seven to ten days on each plot. Where possible, one hundred larvae were hand picked at random from the foliage. These were preserved in 70% alcohol, later separated into instars by head capsule measurements, and dried at 90°F and approximately 2-3% R.H. The larvae were dried to constant weight, then individually weighed with a torsion balance to the closest one-twentieth of a milligram. A total of 1674 larvae were measured for head capsule widths and 1441 were weighed.

Cumulative growth curves were drawn for terminal and radial growth. Little difference in seasonal growth patterns was found between the two species of trees, although the effect of sites previously described was quite distinct. Time of initiation and cessation of growth were similar in all plots except one in a non-outbreak area where a slightly longer growing season occurred because of favorable moisture conditions.

The times of some phenological events for the budworm and the host trees were noted through the season but none showed any important relationships which could be attributed to outbreak or non-outbreak areas. In most cases, the development of one outbreak area was slightly behind that of the other areas.

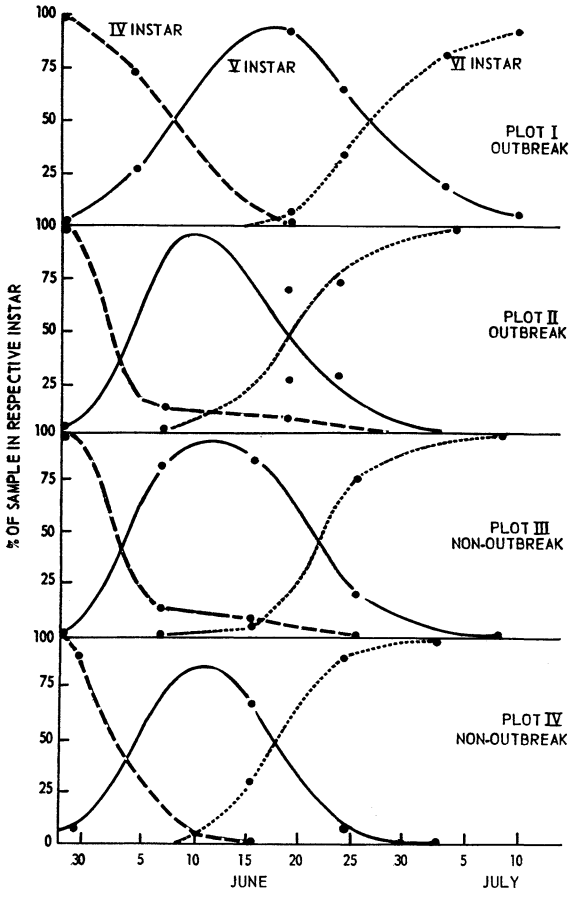


FIG. 10. Curves of the proportion of the population in the respective instars for each plot.

The percentage of the sample in each instar was calculated from head capsule measurements and then plotted according to the time the sample was taken (Fig. 10). Curves were drawn through these points representing the proportion of each instar present at any particular time. Although the larval development differed as much as eight days between the four plots, there seemed to be no consistent relationship between the rate of larval development in outbreak and non-outbreak areas.

The larval developmental rates were also calculated on the basis of body weight. The data on weight were treated with a log (x + 1) transformation which allowed the plotting of regression lines for the various plots. With such a transformation, the assumptions necessary for the derivation of the regression lines and for the application of tests of significance were met. A total of 1441 measurements were used to establish the four lines which appear in Fig. 11. The slope of the line represents the rate of development. These slopes were .0236 and .0283 for the two outbreak areas and .0276 and .0331 for the non-outbreak areas. It is obvious, without any tests of significance, that these developmental rates do not fall into two groups which could account for the restriction of outbreaks to certain areas.

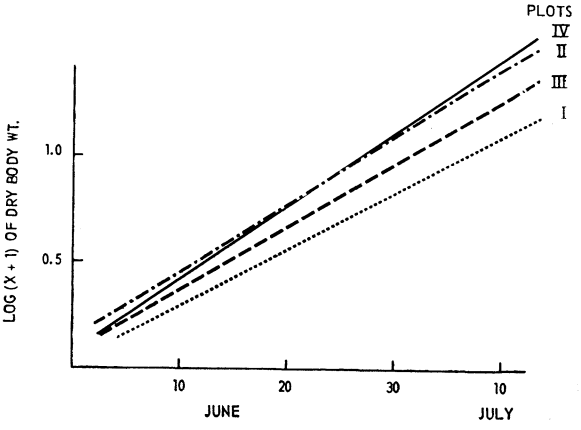


FIG. 11. Log x + 1 transformation of the rate of growth by dry body weight for each plot. Regression lines are plotted by the method of least squares. Plots I and II are outbreak areas and III and IV non-outbreak areas.

As shown in the evaporation study (Fig. 8), 1952 was a wet year in the two-year cycle area. Wet, cold weather tends to equalize the ecoclimates of the different associations, thus largely preventing any differential rate of development of larvae of one association over those of another association. The differences that would occur in development rates during dry years are still unknown.

Hygrothermographs were maintained in the same stands concurrently with the growth and developmental studies for the three years 1952, 1953, and 1954. Highest and lowest minimum temperatures were consistently found in outbreak areas; therefore, late spring frost was discounted as a factor causing population differences between the two areas.

SPRUCE BUDWORM SURVIVAL

The above sections describe outbreak and non-outbreak areas from the standpoint of forest association, site, ecoclimate, phenology, and forest composition in their relation to budworm incidence. From these descriptions, inferences can be made of the environmental factors affecting budworm survival. Unfortunately, it was not possible to determine survival of natural populations in the areas. Populations were so low that sampling to determine survival at the various stages of the life cycle was not practical. As an alternative, trees were artificially infested in the outbreak and

TABLE VI. Survival and mortality rates for fourth to sixth instar larvae and pupae on artificially infested trees

Mortality or Survival Factor	Outbreak				Ave.	Non-out-break				Ave.	Probability of a difference between outbreak and non-outbreak areas.
	1954		1956			1954		1956			
	No.	%	No.	%	%	No.	%	No.	%	%	
Fungus Diseases	0	0	2	5.7	2.0	12	9.1	61	45.5	27.5	>.99
Virus Disease	3	4.5	1	2.9	4.0	15	11.4	11	8.2	9.8	.97
Unknown Mortality	4	6.1	17	48.5	20.8	24	18.2	24	17.9	18.0	.54
Survival Adult	59	89.4	15	42.9	73.3	81	61.3	38	28.4	44.7	>.99

non-outbreak areas, and the survival of these populations was observed closely.

Two cages were set up, one in an outbreak area and the other in a non-outbreak area; each cage was 11′ x 8′ x 8′ and covered two fir trees 7 feet high. These cages were covered with overlapping chicken wire to prevent bird predation without seriously affecting either parasitism or climate. A cloth was stapled on a wooden frame covering the area below the trees. Around the edge of this frame a band of tanglefoot was spread to trap any larvae which fell or spun down and wandered to the edge of the tray. Two 1-foot wooden squares covered with tanglefoot were placed on the roof of each cage to check for any larval drop from trees above.

The budworm used to infest these trees came from a third area, 1 mile east of Field, British Columbia. About 700 fourth-instar larvae were placed upon each tree and weekly counts made until adult emergence. All dead larvae on the frame or trees were immediately placed in gelatin capsules and either held for parasitism or sent to the laboratory for disease identification. The latter part of two life cycles was studied on the same trees, introducing new populations each time. Attempts were made to follow the early part of the life cycle from egg to third instar, but these were unsuccessful.

A survey of parasitism was made in 1954 in two outbreak and one non-outbreak area before the above populations were introduced from the field. Populations were too low for mass collections in the other non-outbreak area Fifth- and sixth-instar larvae were collected and reared until pupation and emergence of either moths or parasites.

The incidence of parasitism found in the areas is presented in Table V. For many years workers in this region have noticed that parasitism of the budworm was low, but no quantitative data had been taken. This survey, based on 2070 budworms taken during a period of decreasing populations, corroborates these observations, so that it is unlikely that parasitism is a primary factor causing the differential rise and fall of budworm populations between outbreak and non-outbreak areas.

TABLE V. Total parasitism appearing in fifth and sixth instar larvae

Area	Per cent parasitism	Number reared
Plot I (Outbreak)	3.09	518
Plot II (Outbreak)	1.85	1135
Plot III (Non-outbreak)	0.24	417
All Areas	1.84	2070

The results of the mortality study of the introduced populations is given in Table VI. Statistically significant differences were found between outbreak and non-outbreak areas in survival, and in mortality due to fungus and virus diseases in both 1954 and 1956. The most important fungus disease was *Beauveria bassiana* (Bals.)

The relationship of the higher incidence of virus infections to the moist ecoclimate of the *Tiarella* association cannot be definitely established, as little is known of the effect of environmental factors on the spread and the infection of diseases caused by virus. It is definitely known, however, that fungus diseases are favored by moist air. Hart and MacLeod (1955) showed that few spores of *Beauveria bassiana* (Bals.) germinated below 94 per cent R.H. With increased humidities there was a corresponding increase in germination.

The average unknown mortality (where no disease or parasitism was present) was similar in both areas. There was, however, considerable difference between years. The unknown mortality during 1954 was 6.1% when calculated evaporation was 3.01, an intermediate year as far as evaporation is concerned (see Fig. 10). In 1956 unknown mortality increased to 48.5% when evap-

oration was 2.32, an unfavorable year for budworm increase. The same trend of unknown mortality did not follow in non-outbreak areas, but the large number of budworms found infected by fungus diseases may have masked a possible increase in the unknown mortality in 1956.

Observations indicated that at least part of the unknown mortality could be attributed to upset behavior patterns. During wet weather larvae were inactive and did not feed, spin, or moult. When the wet weather persisted many larvae died. This is supported by laboratory behavior studies on the one-year cycle budworm (Wellington 1950b). First-instar larvae spun their hibernacula more rapidly at a high rate of evaporation. If the rate of evaporation fell, the time necessary for spinning increased, and the percentage of larvae able to complete their hibernacula decreased until at saturation the larvae were effectively immobilized. When second-instar larvae left their hibernacula in spring, they moved to their feeding sites in the new buds. Their rate of movement was controlled by the rates of evaporation. These larvae moved fastest at a high rate of evaporation; at lower rates the speed of crawling decreased rapidly. The sixth-instar larvae were also sluggish and slow moving at low rates of evaporation and could only feed, move, and develop properly at higher evaporation rates. It can be seen that larvae which live in a dry habitat, such as the *Picea Engelmanni-Abies/Peltigera aphthosa* association, have an advantage over the larvae exposed to lower evaporation rates of a moist plant community.

Greenbank (1956) has pointed out that not only is the success of the spruce budworm related to climate through mortality, but also through changes in fecundity. Larvae that feed on staminate flowers have increased fecundity, and, as discussed earlier, staminate flower production increases in dry years. In addition, during warm dry springs, larvae that develop faster are able to feed more upon young foliage and this increases fecundity.

The budworm is present in endemic numbers throughout most of the mature spruce-fir stands of the region under study. Usually these populations are quite low and no defoliation is noticeable. These studies indicate that the high mortality which keeps the populations on a low level is at least partially attributable directly and indirectly to the high moisture conditions, or conversely, to low evaporation rates. During dry years, evaporation rates are increased, allowing a greater number of larvae to complete development. These evaporation rates are not only determined by the regional weather systems, but also by the habitats of the various stands. The difference in the evaporation rates between the *Peltigera* and the *Tiarella* association increases with any regional increase in evaporation resulting in a comparatively greater 'release' of the budworm in *Peltigera* association.

It has been estimated that the one-year cycle spruce budworm usually requires four or five years of hot dry weather in June and July to increase to outbreak proportions. In the two-year cycle budworm this period would have to be extended to eight or ten years, but with emphasis on every second year when the larvae are in the sixth instar.

Summary

The spruce budworm of the spruce-fir forests in the Canadian Rocky Mountains maintains a two-year life cycle, overwintering in the second and fourth instars. The life cycles are largely coordinated into one brood so that most adults are found during the even numbered years, i.e., 1954, 1956, 1958. While the budworm usually can be found in most of the stands, populations in certain restricted stands are consistently higher. The latter are called outbreak areas and can be recognized easily by marked defoliation and conspicuous red tops. In the non-outbreak areas the budworm may be quite common, and many new shoots may sometimes be defoliated, but extensive defoliation of the trees does not occur.

References

Anonymous. 1947. British Columbia Forest Service Yield Tables. 46 p.

Balch, R. E. 1946. The spruce budworm and forest management in the Maritime Provinces. Canada Dept. Agr., Div. Ent., Proc. Pub. #60 Ottawa. 7 p.

Blais, J. R. 1952. The relationship of the spruce budworm to the flowering condition of balsam fir. Can. J. Zool. 30: 1-29.

Braun-Blanquet, J. (Translated, revised, and edited by G. D. Fuller and H. S. Conard) 1932. Plant Sociology. McGraw-Hill. New York. 439 p.

Colman, E. A. 1950. Manual of instructions for use of the fiberglas soil-moisture instrument. Berkeley Scientific Division of Beckman Instruments Inc. 20 p. Zool. 34: 453-476.

Cook, J. A. 1953. Life history and population studies of the two year cycle spruce budworm, *Choristoneura fumiferana* (Clem.) in Banff, Kootenay, and Yoho National Parks of the Rocky Mountains and reference to the forest composition. Master's Thesis, Univ. New Brunswick, Fredericton, N.B. 78 p.

Daubenmire, R. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecological Monog. 22: 301-330.

Greenbank, D. O. 1956. Role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. 1. Role of Climate. Can. J. Zool. J34: 453-476.

Hart, M. P., and D. M. MacLeod. 1955. An apparatus for determining the effects of temperature and humidity on germination of fungus spores. Can J. Bot. 33: 289-292.

Jaynes, H. A., and C. F. Speers. 1949. Biological and ecological studies of the spruce budworm. J. Ec. Ent. 42: 221-225.

LeBarron, R. K., and G. M. Jemison. 1953. Ecology and silviculture of the Engelmann spruce-Alpine fir type. J. For. 51: 349-352.

Lindsey, A. A. 1955. Testing the line-strip method against full tallies in diverse forest types. Ecology 36: 485-495.

Lutz, H. J., and R. F. Chandler. 1947. Forest Soils. John Wiley London. 514 p.

Mathers, W. G. 1932. Spruce budworm in B.C. For. Chron. 8: 154-157.

Morris, R. F. 1948. How old is a balsam tree? For. Chron. 24: 106-110.

Moss, E. H. 1955. The vegetation of Alberta. Bot. Rev. 21: 493-567.

Poore, M. E. D. 1956. The use of phytosociological methods in ecological investigations. IV. General discussion of phytosociological problems. Jour. Ecology 44: 28-49.

Prebble, M. L. 1945. Spruce budworm. Canada Dept. Agr., Div. For. Biol., Bi-monthly Prog. Rept. 1(4): 2.

Rose, A. H., and J. R. Blais. 1954. A relation between April and May temperatures and spruce budworm emergence. Can. Ent. 86: 174-177.

Turner, K. B. 1952. The relation of mortality of balsam fir by the spruce budworm to forest composition in the Algoma forest of Ontario. Can. Dept. Agr., Publ. 875. 107 p.

Wellington, W. G. 1950a. Effects of radiation on the temperature of insectan habitats. Sci. Agr. 30: 209-234.

———. 1950b. Variations in the silk spinning and locomotor activities of the larvae of the spruce budworm at different rates of evaporation. Trans. Roy. Soc. Can. XLIV, Sec. 3: 89-101.

Westveld, M. 1945. A suggested method for rating the vulnerability of spruce-fir stands to budworm attack. U.S. For. Serv., Northeast. For. Expt. Stn., Proc. Publ. 4 p.