WEATHER AND OUTBREAKS OF THE SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA* (LEPIDOPTERA: TORTRICIDAE)

BY

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ABSTRACT

Weather records from 48 climatological stations across Canada were examined in relation to reported outbreaks of the spruce budworm, Choristoneura fumiferana. *Heat units above 40°F and below 0°F during the overwintering period and above 50°F in the 6-week period following peak third instar were related to population change. Paired comparisons showed that years with increasing populations tended to have lower values for the first two variables and higher values for the last than did years with decreasing populations. Continuous records over a 40-year period for nine climatological stations showed that most expansions in areas of infestation occurred during relatively dry years, and that weather tended to be more favorable during outbreak periods than during non-outbreak periods. Extended periods of favorable weather, plus suitable host stands, appeared to be prerequisites for outbreaks.*

RESUME

L'auteur compara les chiffres obtenus de 48 stations climatologiques à travers le Canada aux invasions connues de la Tordeuse des bourgeons de l'Epinette, Choristoneura fumiferana. *Les unités de chaleur au-dessus de 40°F et sous 0°F durant la période d'hivernation et au-dessus de 50° durant la période de*

6 semaines aprés le sommet atteint par le 3^e stade furent comparées aux changements de population. Ils démontrèrent que pour les années durant lesquelles les populations augmentèrent, les deux premières variables s'avêraient plus basses et la dernière était plus élevée que pour les années de déclin des populations. Les chiffres obtenus durant 40 ans de suite dans 9 stations climatologiques permirent de conclure que la plupart des expansions dans les aires d'infestation se produisirent durant des années relativement sèches et que les conditions météorologiques étaient plus favorables (automnes frais, hivers doux et été chauds et secs) durant les périodes d'invasions. Un temps favorable prolongé, outre des peuplements hôtes suffisants, semblaient nécessaires aux invasions.

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INTRODUCTION

The eastern spruce budworm, *Choristoneura fumiferana* (Clemens), is indigenous to North America and has caused tremendous losses in stands of its principal hosts, balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss) and red spruce (*Picea rubens* Sarg.) (Blais and Martineau 1960, de Gryse 1947, Elliot 1960, Swaine and Craighead 1924). Outbreaks have occurred in most spruce-fir forests in Canada. Growth ring analyses have detected probable outbreaks as early as 1704 (Blais 1968), long before any major interference by man, so the spruce budworm has to be considered a natural part of the ecosystem. However, the depredations of this insect are of major concern in forest management because they are particularly devastating in mature and over-mature stands, those with the greatest commercial value. Fortunately, the intervals between outbreaks in eastern North America are often more than 70 years (Blais 1968), otherwise there would be little commercial timber among the tree species attacked.

Two major factors are believed to be responsible for the relative infrequency of outbreaks: forest composition and weather. Forest composition is probably most important, as major outbreaks do not seem to develop in the absence of mature or over-mature host trees. Outbreaks have occurred in areas where balsam fir is absent or present only in small numbers, such as the Spruce Woods Forest Reserve and Namew Lake area in Manitoba and the Mackenzie River Valley in the Northwest Territories, indicating that the insect can reach outbreak proportions in the absence of balsam fir. Mature and over-mature balsam fir, however, appear to be particularly susceptible to attack, and most recorded outbreaks have probably developed in areas where such trees formed a major component of the stands (Blais 1968, Craighead 1924). Heavy mortality of balsam fir is often caused by severe budworm defoliation for prolonged periods; spruce are also killed, but seem to be able to withstand longer periods of defoliation than balsam fir. Once the balsam fir have been killed, the stands are believed to be less vulnerable to attack, at least until the fir regeneration reach maturity. Swaine (1928) and Graham (1939) recognized the importance of forest composition in the initiation of outbreaks, but also postulated that a period of favorable weather was required for major outbreaks. This postulate was later confirmed by Wellington (1952) and Wellington *et al.* (1950), who showed that outbreaks of the spruce budworm tended to occur when the annual numbers of cyclones was minimal, i.e. during warm dry weather. Further confirmation was provided by Greenbank (1956, 1963), who showed that the spruce budworm outbreaks that began in New Brunswick in 1912 and 1949 were both preceded by dry, sunny summers for 4 or 5 consecutive years.

This paper examines a number of spruce budworm outbreaks in Canada and attempts to determine if there is a relationship between weather conditions and outbreak history. The areas examined are those in which the one-year cycle budworm is the only species, since early records do not distinguish between this insect and the two-year cycle spruce budworm, *Choristoneura biennis* Freeman (Freeman 1967, Shepherd 1961). Information on outbreaks was obtained largely from the Annual Reports of the Forest Insect and Disease Survey (Anonymous 1939-1972), supplemented by information contained in a number of cartographic histories (Blais 1964, Brown 1970, de Gryse 1947, Elliot 1960, Webb *et al.* 1961), while the weather records were those collected by the Atmospheric Envronment Service of Environment Canada[1].

LIFE HISTORY AND LARVAL DEVELOPMENT

The life history of the spruce budworm must be considered when evaluating the possible effects of weather on population trends. Detailed descriptions can be found elsewhere (Craighead 1924, Dowden *et al.* 1948, McGugan 1954, Morris and Miller 1954). A brief description follows. Mating takes place in July or August, eggs are laid on the foliage and hatch in 8-12 days. The larvae then wander briefly before spinning hibernaculae, apparently without feeding, in which they over-winter as second-instar larvae. In the spring, after a period of warm weather, the larvae emerge and mine the old needles or the buds. The small larvae, suspended on silken threads, may disperse at this time, or during the previous fall before the spinning of hibernaculae. After feeding within the mines,

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[1] Published in Monthly Record (Meteorological Observations in Canada). Environment Canada, Atmospheric Environment Service, Information Canada, Ottawa.

the larvae moult and start feeding on the expanding foliage, which is bound together with silken threads, or in the staminate flowers. There are six larval instars. Pupation occurs on the trees and the adults emerge 8-12 days later.

The dates of peak emergence of larvae from hibernaculae vary from year to year and from place to place, as do the dates of peak third instar abundance, when the larvae start to feed on the new foliage. These dates often vary by a month or more, hence the use of fixed time periods does not provide a very satisfactory index of environmental conditions to which the insects are exposed. Several workers have found that the developmental stages under field conditions can be estimated with reasonable accuracy by accumulating the number of heat units above suitable thresholds. In Colorado, the heat units above 42°F provided an estimate of the development of *Choristoneura occidentalis* Freeman (Wagg 1958), while similar results were obtained with a threshold of 37°F for *C. fumiferana* in Minnesota (Bean 1961, Bean and Wilson 1964). Cameron *et al.* (1968) tested Bean's results in New Brunswick and obtained good agreement, although they felt that 40°F might be a better threshold temperature. Further studies in New Brunswick, using a threshold of 42°F, obtained results that were in general agreement with those obtained in Colorado (Miller *et al.* 1971). The results of these four studies are in excellent agreement, considering the range of conditions under which the data were collected (Fig. 1). The dotted line in Fig. 1 is the average of the formulae for the other two, and was considered to provide a reasonable estimate of development in relation to heat units above 40°F. This conclusion is supported by the fact that the three black squares, representing heat units above 40°F for collections of over 20,000 larvae and pupae in Manitoba, fall near this line. Consequently, a developmental threshold of 40°F was used in this study to calculate the dates of peak emergence and third instar abundance. These were estimated to occur when the cumulative heat units above 40°F, based on the Lindsey-Newman (1956) formulae[2], starting 1 March, equalled or exceeded 172 and 381 for emergence and third instar respectively. These values correspond to 220 and 460 heat units above 37°F.

Methods have been devised for estimating the numbers of heat units when only daily maximum and minimum air temperatures are available. The best of these is based on the sine curve (Arnold 1960), followed closely by the triangulation method (Lindsey and Newman 1956). The formulae for the latter method are simple, lending themselves to programming on desk-top computers of limited capacity, hence they have been used throughout this study for calculating the numbers of heat units during the various time periods.

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[2] The numbers of heat units were obtained by summing the degree-day values for the appropriate periods and thresholds. Expressed as degree-days, the Lindsey-Newman formulae are:

$$\begin{aligned} \text{Degree-days} &= \frac{h+m}{2} - t & t &< m; \\ &= \frac{(h-t)^2}{2(h-m)} & m &\leqslant t < h; \\ &= 0 & h &\leqslant t \end{aligned}$$

where h = maximum temperature, m = minimum temperature, and t = threshold temperature.

The lengths of the mining and free-feeding stages vary with the weather. These could be estimated, but would complicate the analyses. Fixed interval lengths of 2 and 6 weeks following estimated peak emergence and third instar respectively were therefore used. These periods will be referred to as spring and summer periods throughout the remainder of this paper.

Little information on the effects of different temperatures on rates of larval development and survival is available. Wellington and Henson (1947) felt that the larvae would not feed when temperatures in the larval environment dropped below about 50°F. This would correspond to air temperatures on cloudy days, but the air temperatures would probably be less on sunny days because of radiant heating. However, there is no practical method for separating cloudy and sunny days for most available records. Although there is some evidence that high temperatures are detrimental to survival (Morris 1963a) and fecundity (Sanders 1967), this was not presently considered and all temperatures above 50°F were treated as being optimum.

WEATHER FACTORS TESTED

In relation to the above life history, the possible effects of weather factors during four periods in the life cycle seemed worthy of examination. These were: fall and early spring temperatures; winter temperatures; spring temperatures following emergence; summer temperatures and precipitation during the large larval period (third to six instar).

Fall temperatures - Warm fall temperatures have an adverse effect on populations of the forest tent caterpillar, *Malacosoma* *disstria* (Hübner), which overwinter as pharate larvae[3] (Ives 1973). The spruce budworm larvae hatch and moult, but otherwise their overwintering location and condition are similar in that they are exposed to the elements for several months before feeding. The larvae are in true diapause, and require at least 20 weeks of cold weather before development can resume in the spring (Harvey pers. comm. 1973), hence there is no premature development as sometimes occurs with the forest tent caterpillar. Nonetheless, warm weather in the fall and early spring before emergence may have an adverse effect because an increased rate of metabolism may exhaust the larvae's limited food reserves. The cumulative number of heat units above 40°F between 15 September and the estimated date of emergence the following year was arbitrarily selected for testing. Although this number contains heat units accumulated in early spring before emergence, most variation occurs in the fall; it will therefore be referred to as fall heat units for the sake of brevity.

Winter temperatures - Declines in spruce budworm populations have been attributed to severe winters (Lambert 1951), but whether these declines were caused by extremely low temperatures or by the cumulative effects of long cold spells is not clear. Other studies (Dowden and Carolin 1950, Miller 1958) have shown overwintering mortality to be as high as 49%, but the cause of this mortality was not determined. Two expressions of temperature were therefore tested, the overwintering minimum temperatures and the cumulative number of

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[3] Fully developed first instar larvae within the eggs.

heat units below 0°F from 1 October to 30 April the following year. No particular significance should be attached to the selection of 0°F as a threshold temperature; it was chosen simply as a convenient value for expressing winter coldness.

Spring temperatures - Warm temperatures as the larvae are emerging from their hibernaculae may increase larval dispersion and hence mortality, but this period is probably too brief to have a detectable effect in the present analysis. However, warm weather following emergence may favor survival, as development will be more rapid. Conversely, frosts may kill the young larvae unless they are cold-hardy. The minimum air temperatures and cumulative heat units above 50°F were therefore derived for the 2-week spring period to determine if either of these possibilities was affecting population trends.

Summer temperatures and precipitation - Warm, dry weather during the large larval period is believed to favor budworm survival, while cool, wet weather is not (Greenbank 1956, 1963; Morris 1963b). In addition, frosts during this period are believed to be responsible for considerable budworm mortality (Atwood 1945, Daviault and Lambert 1946, Dowden *et al.* 1948, Morris and Miller 1954). Four expressions of weather were therefore evaluated for the 6-week summer period: the cumulative number of heat units above 50°F, the minimum air temperatures, the total precipitation, the number of days with .01 in. or more of rain.

VALUES OF FACTORS FOR INCREASING AND DECREASING POPULATIONS

The data on most spruce budworm outbreaks are relatively crude, and it was impossible to determine quantitative population levels from them. However, it was often possible, on the basis of reported defoliation, to select locations for which a year of maximum increase and a year of maximum decrease in an infestation could be determined with reasonable certainty. Weather records were available for 57 infestations (Table I). The approximate locations of the climatological stations were mapped (Fig. 2). Their distribution covers most of the spruce budworm's range in Canada.

For each pair of years, values were calculated for each of the factors outlined in the preceding section and compared by Student's t-test for paired values. To illustrate the variability in the data, the results were also plotted (Fig. 3). No association between the factor and population change is indicated by a more or less equal scattering of points on either side of the dotted line (Fig. 3 A, B, E, and F). A concentration of points above or below the dotted line indicates association between population change and the factor. The differences in heat units during the fall and winter periods were significant at the .05 level, while differences in heat units during the summer period were significant at the .01 level (Fig. 3 G, H, and I). The only other factor that showed any difference was the summer minimum air temperatures. These tended to be slightly higher during years with increasing populations than during years with decreasing populations, but the numbers of killing frosts, $28^{\circ}F$ or less, were identical (7 in both cases). The role of frosts is therefore difficult to determine, and probably depends upon the amount of foliage destroyed, which in turn depends on the stage of foliage growth at the time of the frost. Because of this, and because summer minimum temperatures and summer heat units were correlated ($r = .457$ with 112 d.f., significant at the .01 level) and showed the same trends, summer minimum temperatures have not been considered in further analyses.

These results indicate that cool falls, warm winters and warm summers tend to be associated with increasing populations, while warm falls, cold winters and cold summers tend to be associated with decreasing populations. These associations will be examined more fully in the following section.

HEAT UNITS AND PRECIPITATION IN RELATION TO OUTBREAK HISTORY

The preceding section showed that certain weather factors were associated with changes in population levels of the spruce budworm. To determine if there is a relationship between these factors and known outbreaks of this insect at nine locations (Fig. 2) during a 40-year period, this section presents yearly values for heat units during the fall, winter and summer, and indicates the years with known budworm outbreaks at each location (Fig. 4). The intervals between the first and last years of moderate to severe defoliation in each area have been heavily stippled, even when defoliation during intervening years may have dropped to light, if the outbreaks appeared to be more or less continuous.

The light stippling indicates probable periods of unreported infestation. Barker and Wong (1948) reported receiving empty pupal cases from Fort Simpson in 1947: as they were received in June, they were probably formed in 1946. The 1945 generation of spruce budworm was therefore probably above endemic levels, otherwise there would not be enough pupal cases to attract attention. The probable periods of infestation for Sioux Lookout and Armstrong are based on growth and mortality studies (Elliot 1960).

Although it was not possible to demonstrate that summer precipitation affected population trends, it has been included because other workers (Greenbank 1956, 1963; Morris 1963b) have associated rainfall amounts with population changes.

Examination of Fig. 4 shows that most years with notable expansions in area of infestation (indicated by arrows) had relatively light rainfall during the 6-week summer period. There is a 1-year displacement of summer rainfall and heat units in Figs. 4 and 5, and values are plotted over the year in which the eggs were laid. When summer rainfall was relatively heavy, i.e. Fort Simpson 1956, 1961 and 1962 (actually 1957, 1962 and 1963) and Armstrong 1942 (actually 1943), the summer heat units were near or above average. These results confirm that warm dry summers favor build-up in budworm populations. In addition, however, the trends in fall and winter heat units suggest that conditions during these periods may have had a noticeable effect on outbreak history. Most outbreaks presented were preceded by periods with relatively cool falls and mild winters.

Yearly fluctuations in values for heat units and precipitation make detection of long-term trends difficult. The curves were therefore smoothed somewhat by taking the 3-year moving average and plotting over the third year (Fig. 5). This manipulation emphasizes the trends already mentioned. Except for The Pas, Sioux Lookout, and Armstrong, outbreaks were preceded by cool falls and warm winters. At The Pas, the outbreak remained static from the time of its detection in 1952 until 1956 (1951 and 1955 in Figs. 4 and 5) and then began to expand rapidly for 5 years (Fig. 4). This coincided with a period in which fall, winter, and summer heat units and summer precipitation were generally favorable. Similarly, the years with increasing infestations at Armstrong were accompanied by generally favorable weather. The relationships at Sioux Lookout were not as clear-cut, but the first three years of expansion were accompanied by mostly favorable weather.

In general, there is a strong tendency, as indicated by the arrows, for all four environmental factors to be more favorable during or preceding outbreaks than during non-outbreak periods. Weather conditions at Fort Simpson appear to have been relatively unfavorable during the recorded outbreak. However, except for summer rain, which is comparatively light in this area, conditions were favorable for the 3-year periods ending with the 1956, 1957, 1958, 1961, 1962, 1963 and 1964 generations of the budworm. Similarly, at Grand Falls the relatively small increases in winter heat units for the 3-year periods ending with the 1960 and 1962 generations probably had no effects on population trends, and the remaining factors were favorable. Weather during the outbreaks in both areas was therefore considerably more favorable than the numbers of arrows indicate.

Favorable weather throughout the life cycle therefore seems to be a major factor in the development and continuance of spruce budworm outbreaks. However, unfavorable weather shows no consistent relationship with their termination.

DISCUSSION

One problem encountered was determining when outbreaks started in remote areas, especially during the earlier years. The indicated years of outbreak are probably reasonably accurate as presented, but there may be errors of one or more years. However, these should not be sufficiently large to invalidate the conclusions reached.

Indirectly, Fig. 5 also provides information about the importance of forest composition in determining susceptibility to budworm attack. For example, three periods of favorable weather occurred in the Atikokan area between 1930 and 1950, but no outbreak developed. This area was affected by an extension of the 1911 outbreak in Minnesota, in which extensive mortality was reported (Blais 1968). Presumably, the stands were not favorable to budworm until the 1950's when the fir regeneration were 35 to 40 years old. Similarly, the Maniwaki, Chicóutimi and Grand Falls areas were all subjected to budworm attack during this early outbreak. Although detailed estimates are lacking, it appears that the mortality of balsam fir was heavy in the Chicóutimi area, moderate around Maniwaki and light near Grand Falls (Swaine and Craighead 1924). Thus, although the weather at Chicóutimi and Maniwaki was favorable during the periods generations probably had no effects on population trends, and the remaining factors were favorable. Weather during the outbreaks in both areas was therefore considerably more favorable than the numbers of arrows indicate.

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Much has been written on the spread of spruce budworm outbreaks from one area to another, and on the role that mass migration plays in the initiation of outbreaks in specific areas. There can be no argument that these migrations do occur, and that dispersal is an important factor in the epidemiology of this insect. However, the present findings indicate that outbreaks in widely separated areas build up in response to favorable weather conditions throughout the insect's life cycle and do not depend on long-range dispersal for their initiation. The wide range of weather conditions under which outbreaks develop also implies that different races of spruce budworm have evolved, each capable of withstanding local weather conditions.

Mortality of small larvae, from the time of hatching until the establishment of feeding sites the following spring, is usually high and is probably one of the main reasons why the build-up in populations is slow in relation to the forest tent caterpillar. Morris (1963b) concluded that this mortality was relatively unimportant in determining population trends, yet this study seems to contradict his opinion. However, two points should be kept in mind. Firstly, the study in New Brunswick dealt primarily with outbreak populations, and factors of importance then could quite conceivably be different from those that were important during the initial build-up of populations from the endemic level. Secondly, his studies were confined to one relatively small geographic area, and are not necessarily applicable to the whole geographic range of the spruce budworm. Without supporting biological data it is difficult to assess the validity of the present findings, but the consistency of the results suggests that they are not merely coincidental.

Weather patterns do not seem to offer the same degree of predictability for spruce budworm outbreaks that was found for the forest tent caterpillar (Ives 1973). However, they may still be of some value for predictive purposes. If susceptible stands are present in an area, one should be on the lookout for possible spruce budworm outbreaks whenever several warm dry summers follow or coincide with periods of cool falls and mild winters.

REFERENCES

Anonymous. 1939-1972. Annual Reports of the Forest Insect (and Disease) Survey 1936-1971. Environ. Can., Can. For. Serv., Inf. Can., Ottawa.

Arnold, C.Y. 1960. Maximum-minimum temperatures as a basis for computing heat units. Proc. Am. Soc. Hort. Sci. 76:682-692.

Atwood, C.E. 1945. Summary report of the Forest Insect Survey, Ontario. *In* Annual Report of the Forest Insect Survey (Forest Insect Investigations), 1944. Div. Ent. Sci. Service, Can. Dep. Agric., Ottawa.

Barker, R.B. and H.R. Wong. 1948. Species causing injury at the present time [in the] forested area [of the] Prairie Provinces. *In* Annual Report of the Forest Insect Survey (Forest Insect Investigations), 1947. Div. Ent. Sci. Service, Can. Dep. Agric., Ottawa.

Bean, J.L. 1961. Predicting emergence of second-instar spruce budworm larvae from hibernation under field conditions in Minnesota. Ann. Ent. Soc. Am. 54:175-177.

Bean, J.L. and L.F. Wilson. 1964. Comparing various methods of predicting development of the spruce budworm, *Choristoneura fumiferana*, in northern Minnesota. J. Econ. Ent. 57:925-928.

Blais, J.R. 1964. Account of a recent spruce budworm outbreak in the Laurentide Park region of Quebec and measures for reducing damage in future outbreaks. For. Chron. 40:313-323.

Blais, J.R. 1968. Regional variation in susceptibility of eastern North American forests to budworm attack based on history of outbreaks. For. Chron. 44:17-23.

Blais, J.R. and R. Martineau. 1960. A recent spruce budworm outbreak in the lower St. Lawrence and Gaspé Peninsula with reference to aerial spraying operations. For. Chron. 36:209-224.

Brown, C.E. 1970. A cartographic representation of spruce budworm, *Choristoneura fumiferana* (Clem.), infestation in eastern Canada, 1909-1966. Can. Dep. Fish. For., Can. For. Serv. Publ. 1263.

Cameron, D.G., G.A. McDougall, and C.W. Bennett. 1968. Relation of spruce budworm development and balsam fir shoot growth to heat units. J. Econ. Ent. 61:857-858.

Craighead, F.C. 1924. Studies on the spruce budworm *(Cacoecia fumiferana* Clem.). Pt. II. General bionomics and possibilities of prevention and control. Can. Dep. Agric. Bull. No. 37, N.S. (tech.).

Daviault, L. and R. Lambert. 1946. Species causing injury at the present time [in the] province of Quebec. *In* Annual Report of the Forest Insect Survey (Forest Insect Investigations), 1945. Div. Ent. Sci. Service, Can. Dep. Agric., Ottawa.

de Gryse, J.J. 1947. Noxious forest insects and their control. Reprinted from the Canada Year Book 1947. 14 pp.

Dowden, P.B., W.D. Buchanan, and V.M. Carolin. 1948. Natural control factors affecting the spruce budworm. J. Econ. Ent. 41:457-464.

Dowden, P.B. and V.M. Carolin. 1950. Natural control factors affecting the spruce budworm in the Adirondacks during 1946-1948. J. Econ. Ent. 43:774-783.

Elliot, K.R. 1960. A history of recent infestations of the spruce budworm in northwestern Ontario, and an estimate of resultant timber losses. For. Chron. 36:61-82.

Freeman, T.M. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera:Tortricidae) in North America. I. Some new forms of *Choristoneura* allied to *C. fumiferana*. Can. Ent. 99:449-455.

Graham, S.A. 1939. Forest insect populations. Ecol. Monog. 9:301-310.

Greenbank, D.O. 1956. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. I. The role of climate, Can. J. Zool. 34:453-476.

Greenbank, D.O. 1963. The development of the outbreak. *In* The dynamics of epidemic spruce budworm populations. Mem. Ent. Soc. Can. No. 31.

Ives, W.G.H. 1973. Heat units and outbreaks of the forest tent caterpillar, *Malacosoma disstria* (Lepidoptera:Lasiocampidae). Can. Ent. 105:529-543.

Lambert, R.L. 1951. Important insects [in the] province of Quebec. *In* Annual Report of the Forest Insect Survey, 1950. Div. For. Biol. Sci. Service, Can. Dep. Agric., Ottawa.

Lindsey, A.A. and J.E. Newman. 1956. Use of official weather data in springtime - temperature analysis of an Indiana phenological record. Ecology 37:812-823.

McGugan, B.M. 1954. Needle-mining habits and larval instars of the spruce budworm. Can. Ent. 86:439-454.

Miller, C.A. 1958. The measurement of spruce budworm populations and mortality during the first and second larval instars. Can. J. Zool. 36:409-422.

Miller, C.A., D.C. Eidt, and G.A. McDougall. 1971. Predicting spruce budworm development. Environ. Can., Can. For. Serv., Bi-mon. Res. Notes 27(5):33-34.

Morris, R.F. 1963a. The development of predictive equations for the spruce budworm based on key-factor analysis. *In* The dynamics of epidemic spruce budworm populations. Mem. Ent. Soc. Can., No. 31.

____________ 1963b. The analysis of generation survival in relation to age-interval survival in the unsprayed area. *In* The dynamics of epidemic spruce budworm populations. Mem. Ent. Soc. Can., No. 31.

Morris, R.F. and C.A. Miller. 1954. The development of life tables for the spruce budworms. Can. J. Zool. 32:283-301.

Sanders, C.J. 1967. Low fecundity of the spruce budworm attributed to unusually high temperatures during immature stages. Can. Dep. For. Rural Devel., Can. For. Serv., Bi-mon. Res. Notes 23(3):19.

Shepherd, R.F. 1961. A comparison of the developmental rates of one-and two-year cycle spruce budworm. Can. Ent. 93:764-771.

Swaine, J.M. 1928. Forest entomology and its development in Canada. Can. Dep. Agric. Pamph. No. 97. 20 pp.

Swaine, J.M. and F.C. Craighead. 1924. Studies on the spruce budworm *(Cacoecia fumiferana* Clem.). Pt.I. A general account of the outbreak, injury and associated insects. Can. Dep. Agric. Bull. No. 37, N.S. (tech.).

Wagg, J.W.B. 1958. Environmental factors affecting spruce budworm growth. For. Lands Res. Cent., Corvallis, Oreg. Res. Bull. No. 11. 27 pp.

Webb, F.E., J.R. Blais, and R.W. Nash. 1961. A cartographic history of spruce budworm outbreaks and aerial forest spraying in the Atlantic Region of North America, 1949-1959. Can. Ent. 93:360-379.

Wellington, W.G. 1952. 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.

Wellington, W.G. and W.R. Henson. 1947. Notes on the effects of physical factors on the spruce budworm, *Choristoneura fumiferana* (Clem.). Can. Ent. 79:168-170, 195.

Wellington, W.G., J.J. Fettes, K.B. Turner, and R.M. Belyea. 1950. Physical and biological indicators of the development of outbreaks of the spruce budworm. *Choristoneura fumiferana* (Clem.) (Lepidoptera:Tortricidae). Can. J. Res. (D) 28:308-331.

Table I. Climatological stations used for comparing weather records pertaining to increasing and decreasing infestations of the spruce budworm. The numbers show the approximate locations of the stations in Fig. 2.

Climatological Stations		Years Compared		Climatological Stations		Years Compared	
Number	Location	Increasing infestations	Decreasing infestations	Number	Location	Increasing infestations	Decreasing infestations
British Columbia				Ontario (cont'd)			
1	Smith River	1961-62	1965-66	26	North Bay	1939-40	1945-46
Northwest Territories				27	Pembroke	1941-42	1945-46
2	Fort Norman	1954-55	1958-59			1948-49	1949-50
3	Fort Simpson	1961-62	1965-66		(Petawawa)	1950-51	1951-52
4	Fort Smith	1962-63	1965-66	28	Uxbridge	1952-53	1959-60
Alberta						1962-63	1967-68
5	Fort Vermilion	1963-64	1967-68	29	Kingston	1944-45	1946-47
Saskatchewan				30	Brockville	1944-45	1945-46
6	Island Falls	1960-61	1968-69	Quebec			
7	Cumberland House	1959-60	1963-64	31	Cadillac	1943-44	1949-50
8	Rosthern	1960-61	1963-64	32	Maniwaki	1943-44	1949-50
9	Merryflat	1957-58	1958-59	33	Parent	1943-44	1949-50

Table I - Cont'd

		1960-61	1961-62	34	La Tuque	1947-48	1951-52
Manitoba						1952-53	1957-58
10	Flin Flon	1957-58	1968-69	35	Roberval	1946-47	1950-51
11	The Pas	1955-56	1968-69			1953-54	1957-58
12	Dauphin	1959-60	1961-62	36	Chicóutimi	1953-54	1957-58
13	Cypress River	1939-40	1941-42	37	La Malbaie	1954-55	1955-56
		1943-44	1948-49	38	Cap Chat	1953-54	1956-57
		1956-57	1957-58	39	Gaspé	1954-55	1957-58
14	Gimli	1954-55	1958-59	40	Port Daniel	1953-54	1957-58
15	Great Falls	1954-55	1957-58	41	Matapedia	1950-51	1957-58
16	Sprague	1955-56	1957-58	New Brunswick			
Ontario				42	Grand Falls	1952-53	1958-59
17	Kenora	1949-50	1958-59	43	Chatham	1952-53	1957-58
18	Sioux Lookout	1951-52	1959-60	44	Chipman	1964-65	1965-66
19	Atikokan	1954-55	1962-63	45	Fredericton	1955-56	1960-61
20	Armstrong	1942-43	1948-49	Nova Scotia			
21	Schreiber	1953-54	1961-62	46	Ingonish Beach	1952-53	1957-58
22	Franz	1939-40	1945-46	Prince Edward Island			
23	Kapuskasing	1943-44	1949-50	47	Charlottetown	1952-53	1955-56
24	Timmins	1941-42	1945-46			1956-57	1958-59
25	Sudbury	1928-29	1931-32	48	Summerside	1953-54	1955-56

Fig. 1. Budworm development in relation to heat units above various thresholds. (1) - Above 42°F in Colorado. (2) - Above 37°F in Michigan. (3) - Average of (1) and (2). Open circles - Above 37°F in New Brunswick. Solid circles - Above 42°F in New Brunswick. Solid squares - Above 40°F in Manitoba. For convenience, pupae and adults have been assigned instar values of 7 and 8, respectively.

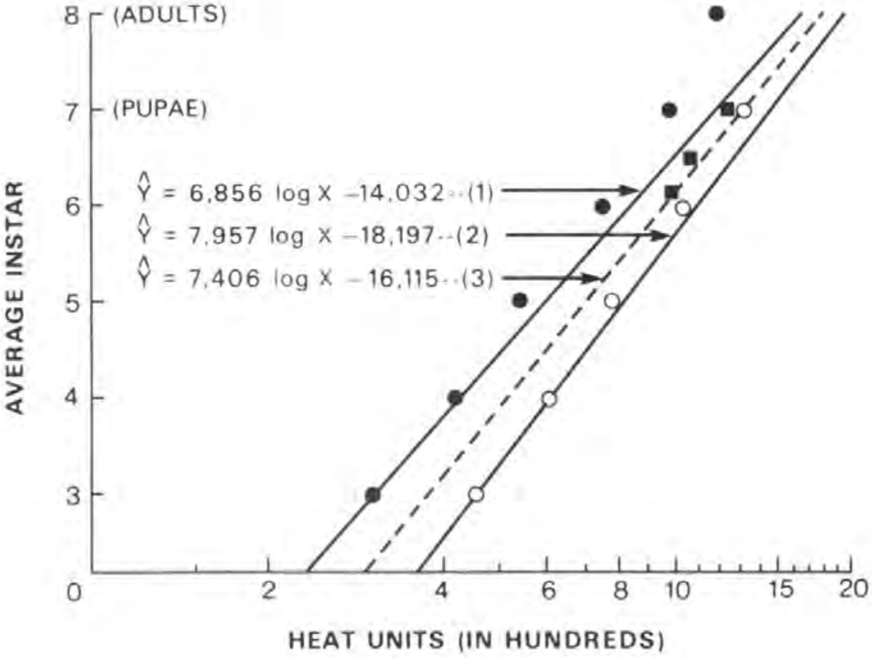
8 (ADULTS)
7 (PUPAE)
6
5
4
3
0
AVERAGE INSTAR
$\hat{Y}$ = 6,856 log X −14,032··(1)
$\hat{Y}$ = 7,957 log X −18,197··(2)
$\hat{Y}$ = 7,406 log X − 16,115··(3)
2
4
6
8
10
15
20
HEAT UNITS (IN HUNDREDS)

Figure 1

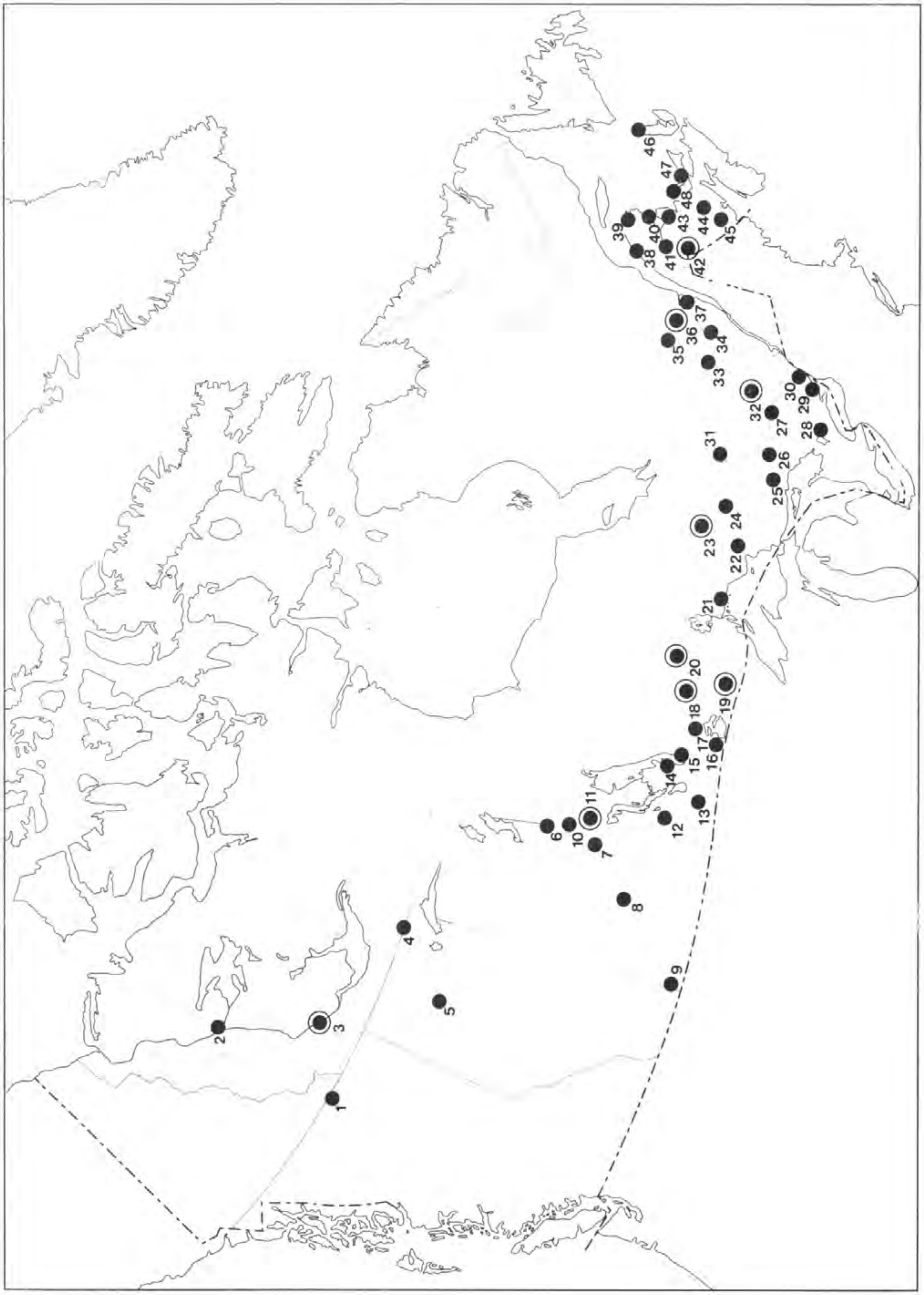
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48

Figure 2

Fig. 3. Values of nine weather-related variables for increasing (Y-axis) and decreasing (X-axis) populations of the spruce budworm. A. Winter minima (°F). B. Minima (°F) in 2-week period following estimated emergence. C. Minima (°F) in 6-week period following estimated peak third instar. D. Heat units above 50°F (in hundreds) in 2-week period following estimated emergence. E. Rainfall (in inches) in 6-week period following estimated peak third instar. F. Numbers of days with .01 in. or more of rain in 6-week period following estimated peak third instar. G. Heat units above 40°F from 15 September to estimated emergence. H. Heat units below 0°F (in hundreds) from 1 October to 30 April. I. Heat units above 50°F (in hundreds) in 6-week period following estimated peak third instar. D = mean difference (increasing-decreasing), t = Student's t for paired comparisons, p = probability of a larger t, sign ignored.

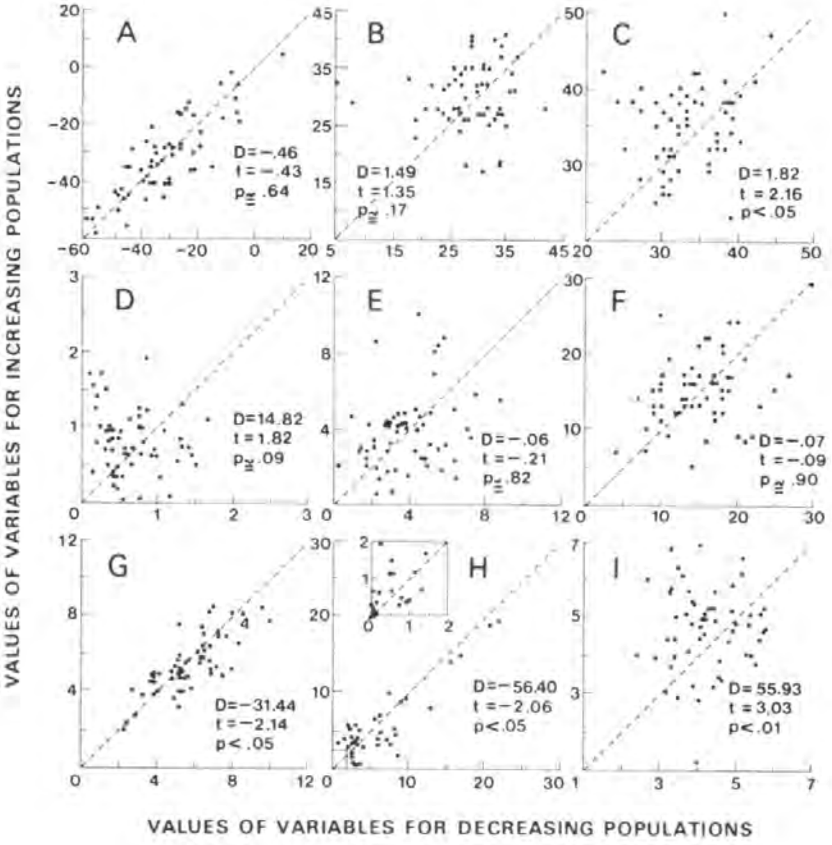
VALUES OF VARIABLES FOR INCREASING POPULATIONS
VALUES OF VARIABLES FOR DECREASING POPULATIONS
A
D=−.46
t=−.43
p≅.64
20
0
-20
-40
-60
-40
-20
0
20
B
D=1.49
t=1.35
p≅.17
45
35
25
15
5
15
25
35
45
C
D=1.82
t=2.16
p<.05
50
40
30
20
30
40
50
D
D=14.82
t=1.82
p≅.09
3
2
1
0
1
2
3
E
D=−.06
t=−.21
p≅.82
12
8
4
0
4
8
12
F
D=−.07
t=−.09
p≅.90
30
20
10
0
10
20
30
G
D=−31.44
t=−2.14
p<.05
12
8
4
0
4
8
12
H
D=−56.40
t=−2.06
p<.05
30
20
10
0
10
20
30
2
1
0
1
2
I
D=55.93
t=3,03
p<.01
7
5
3
1
3
5
7

Figure 3

Fig. 4. Fall, winter, and summer heat units and summer rain for successive generations of the spruce budworm at nine locations. Known outbreak periods are heavily stippled. Probable outbreak periods are lightly stippled. Dotted lines are the 40-year means for the respective variables. Arrows indicate those generations with notable expansions in areas of infestation.

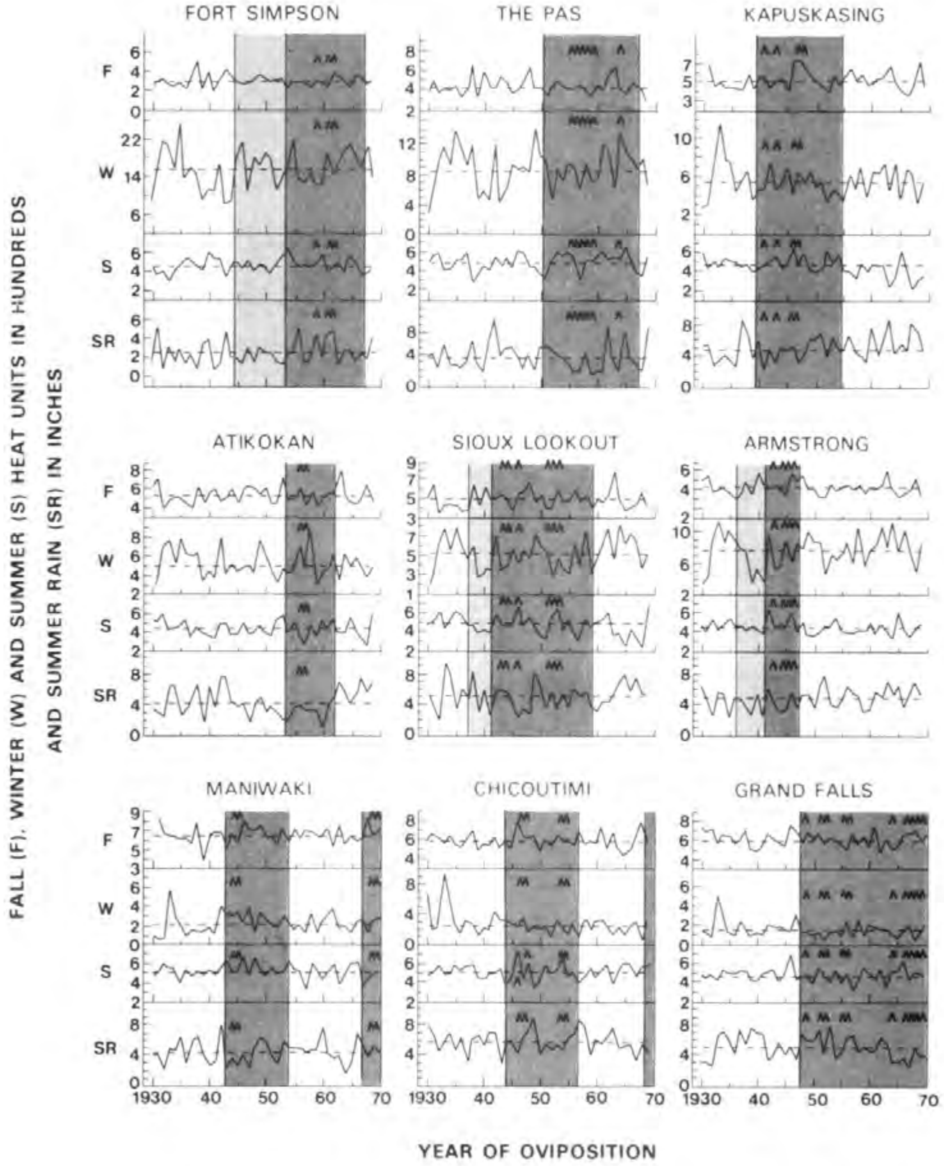
FORT SIMPSON
THE PAS
KAPUSKASING
ATIKOKAN
SIOUX LOOKOUT
ARMSTRONG
MANIWAKI
CHICOUTIMI
GRAND FALLS
F
W
S
SR
FALL (F), WINTER (W) AND SUMMER (S) HEAT UNITS IN HUNDREDS
AND SUMMER RAIN (SR) IN INCHES
1930
40
50
60
70
YEAR OF OVIPOSITION

Figure 4

Fig. 5. Three year moving averages for fall, winter, and summer heat units and summer rain, plotted over the third year, for successive generations of the spruce budworm at nine locations. Known outbreak periods are heavily stippled. Probably outbreak periods are lightly stippled. Dotted lines are the 40-year means for the respective variables. Arrows indicate the 3-year periods when none of the variables deviated, in an unfavorable direction, from the 40-year means by more than 10%.

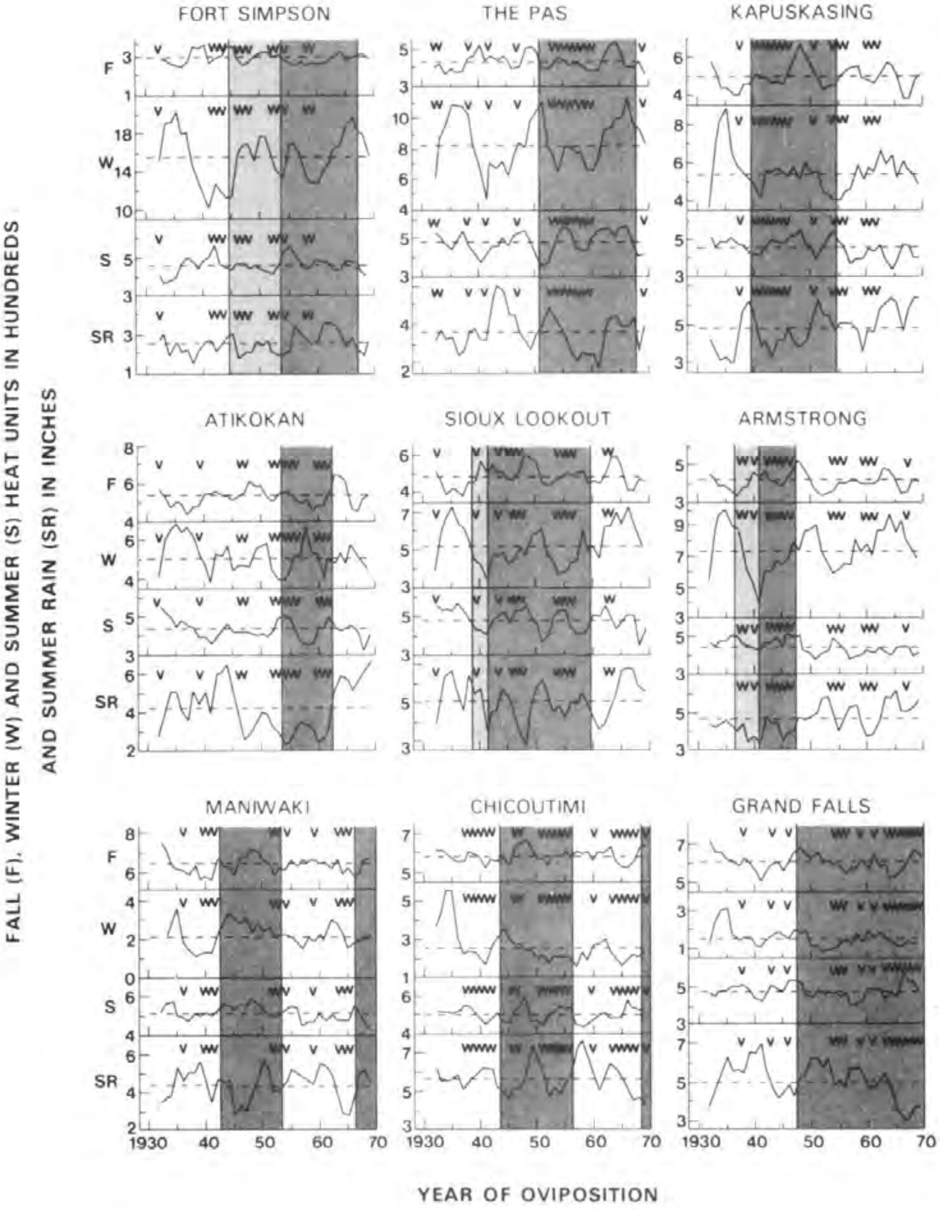
FORT SIMPSON
THE PAS
KAPUSKASING
ATIKOKAN
SIOUX LOOKOUT
ARMSTRONG
MANIWAKI
CHICOUTIMI
GRAND FALLS
F
W
S
SR
FALL (F), WINTER (W) AND SUMMER (S) HEAT UNITS IN HUNDREDS
AND SUMMER RAIN (SR) IN INCHES
1930
40
50
60
70
YEAR OF OVIPOSITION

Figure 5