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RELATING WEATHER TO OUTBREAKS OF WESTERN SPRUCE BUDWORM, *CHORISTONEURA OCCIDENTALIS* (LEPIDOPTERA: TORTRICIDAE), IN BRITISH COLUMBIA

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Abstract

Can. Ent. 116: 375–381 (1984)

The relationship of western spruce budworm outbreaks and population collapse to weather parameters was examined using long term weather records from two stations in the budworm outbreak area of British Columbia and outbreak patterns obtained from Forest Insect and Disease Survey records and from tree stem analyses.

Outbreaks were associated with warm dry summers in conjunction with synchrony of larval emergence and bud flush. Collapse of the last two outbreaks was clearly associated with extreme high temperatures following moth flight. Collapse of the earlier outbreaks may have been due to asynchrony between larval emergence and bud flush.

Résumé

Les auteurs ont étudié le rapport entre des paramètres météorologiques et les pullulations et effondrements des populations de la tordeuse occidentale de l'épinette. Ils ont utilisé pour leur analyse les données météorologiques enregistrées sur une longue période par deux stations situées dans la zone d'infestations en Colombie-Britannique et les données sur les caractéristiques des infestations obtenues des relevés des insectes et des maladies des arbres et des analyses de la tige.

Ils ont trouvé que les pullulations étaient reliées à des étés secs associés au synchronisme de l'apparition des larves et de la sortie des bourgeons. L'effondrement des deux dernières pullulations est nettement associable à des températures élevées extrêmes après l'envol des papillons. La non-coïncidence de l'émergence des larves et de la sortie des bourgeons a pu causer l'effondrement des pullulations antérieures.

Introduction

Defoliation of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, by the western spruce budworm, *Choristoneura occidentalis* Freeman, along with other insect damage in British Columbia, is recorded annually from the air by the Forest Insect and Disease Survey (FIDS) of the Canadian Forestry Service. Patterns of defoliation vary markedly from outbreak to outbreak. FIDS records and a report by Silver (1960), supplemented by stem analyses (Thomson and Van Sickle 1980), indicate two main centres of defoliation in British Columbia, a northern one centered near Pemberton, and a southern one around Hope. The objective of the present study was to detect biologically significant variations in long-term weather records at the two centres of defoliation, and to relate these to observed regional outbreak patterns.

Many studies of weather effects on the spruce budworm, *C. fumiferana* (Clem.), have been reported (Wellington *et al.* 1947, 1950; Greenbank 1956; Ives 1974, 1981) but few on the western budworm (Wagg 1958; Shepherd 1961; Hard *et al.* 1980). In an analysis of relationships of western spruce budworm population dynamics, Thomson (1979) emphasized the importance of weather effects, particularly the synchrony between larval emergence and bud flush of the host tree.

The analysis of weather effects on *C. occidentalis* in the mountainous terrain of British Columbia from a broad regional perspective using historical weather records has been made possible by two recently reported studies. Thomson and Moncrieff (1982) evaluated the degree-day requirements for Douglas-fir bud burst, and Thomson *et al.* (1983) have developed a method of predicting budworm development over an elevation range wherein a temperature–elevation relationship is established to estimate temperatures at particular locations.

Methods

Daily temperature and precipitation records were obtained for Hope (Hope Airport 1934–1978) and Pemberton (Pemberton Meadows 1912–1968; Pemberton BCFS 1969–1978). Missing temperature and precipitation data were estimated by multiple regression from neighbouring station records.

Budworm development over a range of elevations was predicted for the Pemberton region as described by Thomson *et al.* (1983). Development was estimated only at the station elevation in the Hope region, because of the varying degree of coastal influence which makes projections to higher elevations difficult as described in that study. Date of first bud flush and first tree flush of Douglas-fir was similarly estimated, as described by Thomson and Moncrieff (1982).

In addition, heat units were calculated above 5.5°C (42°F), the normal threshold of budworm larval development, and also heat units above 23.9°C (75°F) for the periods 1–14, 15–28, and 28+ days after moth flights. The 23.9°C threshold was selected arbitrarily to identify extremely warm temperatures. The last date on which the minimum temperature fell below 0°C was used as an indication of the probable date of last frost. The weather parameters indicated in Table I were then calculated for each of the weather records.

Budworm outbreak history from 1949 was evaluated from FIDS records, and from stem analysis for earlier outbreaks (Thomson and Van Sickle 1980; Alfaro *et al.* 1982). Dates obtained through stem analysis refer only to the history within specific stands and not to the outbreak as a whole. Weather effects were considered separately for the two critical phases of the population cycle, release and collapse, as population response to a particular factor may be different during different phases. Release was indicated by the first year of widespread defoliation in a region, and collapse by the widespread disappearance of defoliation. For outbreaks indicated by stem analyses in individual stands, these dates are approximate for the region as a whole.

Periods of defoliation, from release to collapse, were identified as follows:

1970–77	(Pemberton region)
1971–present	(Hope region)
1952–58	(Pemberton region)
1942–44	(Pemberton region)
1927–29	(Pemberton region)

The 1950's outbreak at Pemberton extended into the Anderson river area, intermediate in position between Hope and Pemberton, but the two earlier outbreaks did not (Van Sickle *et al.* 1983). Studies of both FIDS aerial defoliation survey records and stem analysis indicate the last year of defoliation, and this is the year cited above. However, the actual collapse of the population may have been due to mortality of early larval instars in the subsequent year.

Weather parameters in Table I were related, individually and in combination, to the release and collapse phases of the above periods of defoliation. Graphical procedures similar to those described by Cramer (1962) (e.g. Fig. 1) were also used to study weather variables in combination. No statistical procedures were used, due to the few outbreaks involved and the possibility of spurious results from such analyses. Visual inspection of the pattern of population trend in relation to climatic fluctuations was considered most appropriate (Royama 1978).

In the present study, outbreaks are considered only in terms of appearance or disappearance of region-wide defoliation, and do not reflect fluctuations in population density or degree of defoliation. For example, during an outbreak, a factor which acts early in the year may greatly reduce populations, but leave sufficient larvae to cause continuing defoliation and other factors may enhance or reduce budworm survival without changing the region-wide defoliation status. Similarly, the analysis would not detect a gradual pre-outbreak increase in population which did not reach a level resulting in visible defoliation.

Table I. Climatological and phenological parameters examined. (Derived parameters obtained from weather station records of maximum and minimum temperatures and precipitation, using heat unit accumulations above 5.5°C to predict dates)

General effects
Average daily temperature and precipitation for June–July
Average daily temperature and precipitation for December–February
Last date with temperatures less than 0°C
Minimum temperature experienced by each life stage
Average daily temperature experienced by each stage
Total precipitation experienced by each stage
Maximum daily precipitation experienced by each stage
Number of days of precipitation experienced by each stage
Days from March 1 to occurrence of each life stage
Days duration of each life stage
Days duration from emergence to moth
Days from moth flight in year *n* to larval emergence in year $n + 1$
Phenological effects
Days from January to first bud flush
Days from emergence to first bud flush
% development of first bud at emergence
Days from January 1 to first tree flush
Days from L3 to first tree flush
% first tree flush at L3
Days from first bud to first tree flush
Fall heat unit effects
Degree days greater than 23.9°C in 14 days following moth flight
Degree days greater than 23.9°C 15–28 days following moth flight
Degree days greater than 23.9°C 28+ days following moth flight
Total degree days greater than 23.9°C following moth flight

Results and Discussion

All four outbreaks at Pemberton and the single outbreak at Hope were preceded by a warm dry summer (Fig. 1) in conjunction with a particular synchronization of larval emergence and first bud flush (Fig. 2). First bud flush is an indicator that most buds are sufficiently swollen to permit mining by the larvae.

Larval emergence preceded bud flush by an average of 14 days at Pemberton. All four outbreaks at Pemberton followed, or were contemporaneous with, years in which larval emergence preceded first bud flush by an abnormally long (for Pemberton) interval. These extreme years also coincided with years of warm dry summers. On the other hand, those years in which dry summers did not follow such extremes did not result in outbreaks. Extreme asynchronization occurred at the approximate time of collapse of the earlier outbreaks at Pemberton. There was a greater delay between emergence and bud flush at Hope (average 24 days) than at Pemberton. Here the outbreak followed a warm dry summer and a separation of emergence and bud flush which was abnormally brief for the region.

The data are consistent with the hypothesis that there exists an optimal phenological relationship of larval emergence and bud flush which results in maximum survival of the bud-mining larvae. With suboptimal phenology, insufficient larvae survive to benefit from favourable summer conditions, and no outbreak follows such warm dry summers. For example, neither 1950 at Pemberton, nor 1969 at Hope, were immediately followed by outbreaks (Fig. 1). Conversely, an average or cool summer may not permit sufficient survival for optimal phenology alone to lead to an outbreak. The optimal phenology must

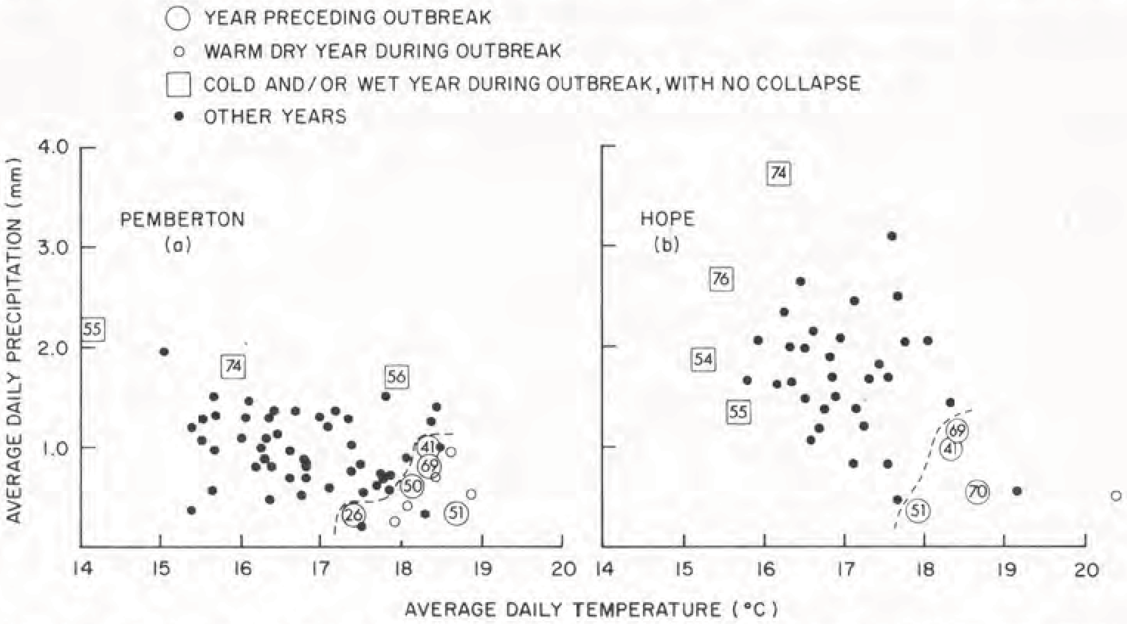

FIG. 1. Scatter diagram of June to July average daily temperature and precipitation in different years for (a) Pemberton and (b) Hope. Warm dry years preceding outbreaks, and cold wet years occurring during outbreaks without causing collapse, are identified.

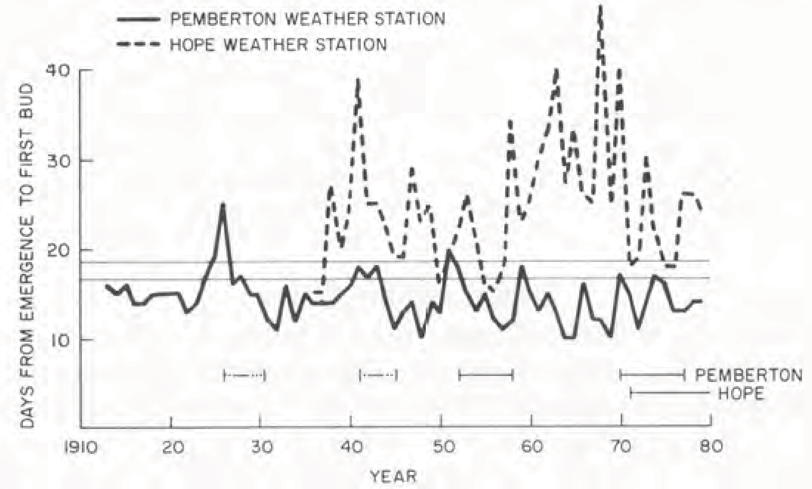

FIG. 2. Relative phenology of larval emergence and bud flush at Pemberton and Hope weather stations. Years of defoliation are indicated by the bars (gaps indicate uncertainty). A 17–18 day separation of emergence and flush is indicated.

lie between the average for Pemberton and Hope; i.e. between 14 and 24 days, and is probably close to the 17–18 days which preceded all recorded outbreaks. Release of budworm populations by weather in a single year may be much more likely in *C. occidentalis* than *C. fumiferana* due to the much higher endemic levels of western spruce budworm on Douglas-fir.

The pattern of separation between bud flush and larval emergence predicted over a range of elevations was very similar to that of Pemberton station. This suggests that although the date of emergence and bud flush may vary over the elevation range in a particular year, the relative timing is generally not affected significantly, assuming that the heat unit requirements used for bud flush evaluation are generally applicable. The degree-day requirements for bud flush established by Thomson and Moncrieff (1982) are based on results for a single stand.

Cold or wet summers were not related to outbreak collapse (Fig. 1). No relationship between December–February weather conditions and release phase was detected, nor was there any indication of a collapse following late frosts. Ives (1981) indicated that *C. fumiferana* collapses were associated with late spring frosts. Blais (1981), however, reported that while late frosts caused considerable damage to foliage, they did not seriously affect budworm populations.

Heavy rains may stimulate the larvae to drop out of the foliage (Wellington and Henson 1947; Henson 1950). However, average temperature, total precipitation, maximum daily precipitation, and number of wet days experienced by each stage were not related to outbreak release or collapse in British Columbia. Temperature variations resulted in different timing and duration of each stage, but these were not related to the outbreak cycle.

Based on experimental results of McMorran (1973), Thomson (1979) suggested that fall weather might influence survival. The nutritional reserves contained in the budworm egg are used for development of the embryo, eclosion, first instar dispersal, hibernaculum formation, moulting to second instar, overwintering for up to 9 months, emergence from the hibernaculum, second instar dispersal, and final location and penetration of a needle or bud. McMorran's results suggested that a long period of warm weather in the fall may result in depletion of these nutritional reserves to the extent that, after emergence from the hibernacula in the spring, the larvae have insufficient nutritional reserves to disperse and mine a needle or bud. Effects of warm periods are indicated in Fig. 3 which shows the total heat units > 23.9°C calculated for Pemberton and Hope weather stations, and predicted for the 600 m elevation at Pemberton, from the time of moth flight.

Collapse of the 1950's outbreak is associated with an extremely warm fall. A similar warm period occurred in 1977 at Pemberton, while at Hope this period was not unusually warm; 1977 was the last year of defoliation in the northern (Pemberton) area, while the outbreak continued in the southern (Hope) area.

The timing of a warm period is critical, as it could instead have the effect of releasing the budworm population (Fig. 1). An exceptionally warm dry spell at one particular time acts on a range of life stages at different elevations, unless it occurs late enough that oviposition is complete at all elevations.

At such time of extreme adverse conditions, the budworm will survive in refugia which may be either spatial, such as cooler high elevations, or temporal, due to extremely late developing individuals. The warm temperature effect was calculated from the estimated date of 50% moth flight. At this time, some individuals would still be in the pupal or even late larval stage.

Defoliation rarely occurs in valley bottoms although field observations indicate that many eggs may be laid there as a result of moth dispersal from upslope populations. Eggs laid in the valley bottoms by invading moths are subjected to much higher temperature than at the main population centre (600 m), augmenting effects of sub-optimal phenology in the valley bottoms.

Summary

The analysis is based on the premise that release and collapse of populations result from extreme climatic conditions, and was therefore carried out only in relation to the appearance or disappearance of region-wide defoliation. Fluctuations in populations or defoliation levels during outbreaks were not considered. Hard *et al.* (1980), in a study of fluctuations of defoliated area in relation to weather, did not include release or collapse years in their analyses, and also excluded some years of unexpectedly low defoliation levels.

Outbreaks of spruce budworm in British Columbia appear to be related to warm dry summers in conjunction with an optimal synchrony between larval emergence and bud

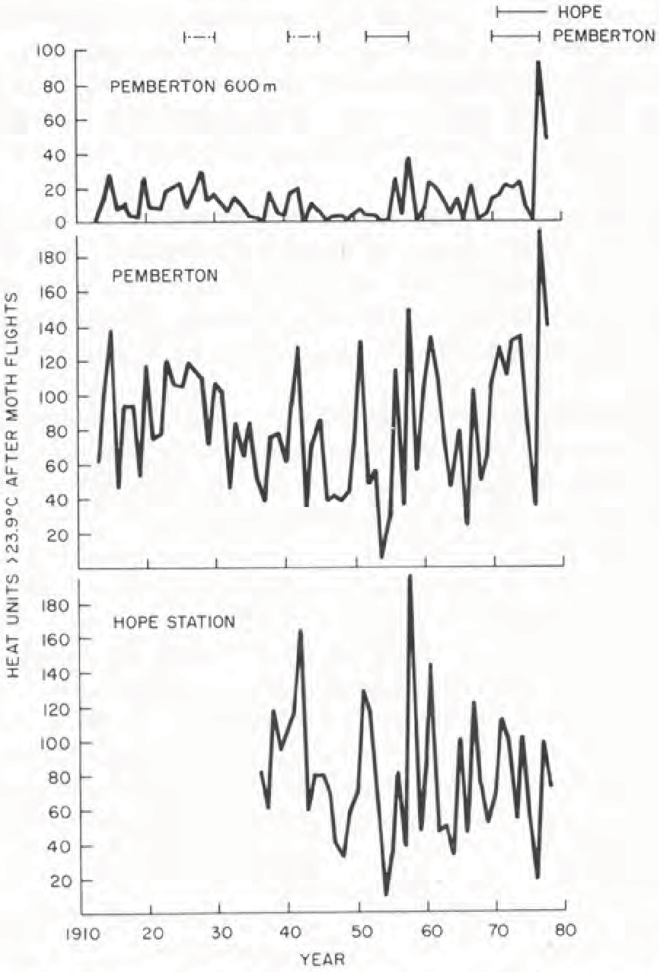

FIG. 3. Fall temperatures following moth flight, as indicated by accumulated heat units > 23.9°C, calculated for Pemberton and Hope weather stations, and estimated for the 600 m elevation at Pemberton. Years of defoliation are indicated by the bars at the top of the figure (gaps indicate uncertainty).

flush. Collapse of the 1950's and 1970's outbreaks coincided with extremely high autumn temperatures following moth flight.

The effects of weather on population outbreak and collapse can be inferred from standard weather and insect survey data if one takes into account topographic variation in climate and applies simple heat unit phenological models. Detailed studies at the stand level are required to confirm and refine the suggested relationships. Finally, the variability of weather factors and consequent effects on budworm outbreak dynamics within a region need to be studied by examining regional homogeneity of weather factors and modification by topography using synoptic weather patterns as well as station climate records.

References

Alfaro, R. I., G. A. Van Sickle, A. J. Thomson, and E. Wegwitz. 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. *Can. J. For. Res.* **12**: 780–787.

Blais, J. R. 1981. Effects of late spring frosts in 1980 on spruce budworm and 13 host trees in the Laurentian Park Region of Quebec. *Can. For. Serv. Res. Notes* **1**: 16–17.

Cramer, H. H. 1962. Moeglichkeifen der Forstschaedlingsprognose mit Hilfe meteorologischer Daten. [English title: The possibility of forecasting outbreaks of forest pests with the aid of meteorological data.] Schriftenreihe der Forstlichen Abteilung der Albert-Ludwigs-Universitaet, Freiburg im Breisgau.

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.

Hard, J., S. Tunnock, and R. Eder. 1980. Western spruce budworm defoliation trend relative to weather in the Northern Region, 1969-1979. *U.S. Dep. Agric. For. Serv., Northern Region, St. & Private For. Rep.* 80-4.

Henson, W. R. 1950. The means of dispersal of the spruce budworm. Ph.D. Thesis, Yale University.

Ives, W. G. H. 1974. Weather and outbreaks of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. For. Serv., North. For. Res. Centre, Inf. Rep.* NOR-X-118.

——— 1981. Environmental factors affecting 21 forest insect defoliators in Manitoba and Saskatchewan, 1945–69. *Can. For. Serv., North. For. Res. Centre, Inf. Rep.* NOR-X-233. 142 pp.

McMorran, A. 1973. Effects of pre-storage treatment on survival of diapausing larvae of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. Ent.* **105**: 1005–1009.

Royama, T. 1978. Do weather factors influence the dynamics of spruce budworm populations? *Can. For. Serv. Bi-mon. Res. Notes* **34**: 9–10.

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

Silver, G. T. 1960. Notes on a spruce budworm infestation in British Columbia. *For. Chron.* **36**: 362–374.

Thomson, A. J. 1979. Evaluation of key biological relationships of western budworm and its host trees. *Can. For. Pacif. For. Res. Cen. Inf. Rep.* BC-X-186. 19 pp.

Thomson, A. J. and S. M. Moncrieff. 1982. Prediction of bud burst in Douglas-fir by degree-day accumulation. *Can. J. For. Res.* **12**: 448–452.

Thomson, A. J. and G. A. Van Sickle. 1980. Estimation of tree growth losses caused by pest activity. *Can. J. For. Res.* **10**: 176–182.

Thomson, A. J., J. W. E. Harris, R. H. Silversides, and R. F. Shepherd. 1983. Effects of elevation on the rate of development of western spruce budworm (Lepidoptera: Tortricidae) in British Columbia. *Can. Ent.* **115**: 1181–1187.

Van Sickle, G. A., R. I. Alfaro, and A. J. Thomson. 1983. Douglas-fir height growth affected by western spruce budworm. *Can. J. For. Res.* **13**: 445–450.

Wagg, J. W. B. 1958. Environmental factors affecting spruce budworm growth. *Res. Bull.* 11. Forest Lands Research Center, Corvallis, Oregon.

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.

Wellington, W. G., T. 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.

(Received 20 June 1983; accepted 16 August 1983)