Spatial synchrony of the two-year cycle budworm outbreaks in central British Columbia, Canada

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Outbreaks of forest defoliating insects are usually synchronized over a large spatial scale. Observed records of past outbreaks are usually short and incomplete, therefore long proxy data are useful for better understanding of the spatial synchrony. In this study, we developed tree-ring proxy records of two-year cycle spruce budworm (*Choristoneura biennis* Freeman) outbreaks in central British Columbia, Canada, and examined the spatial patterns of past outbreaks. This budworm is a major defoliating insect of the interior spruce (*Picea engelmannii* Parry × *P. glauca* Moench) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) forests in the Prince George Region of British Columbia. Four outbreaks occurred in relatively close synchrony over the entire region in the period 1880–1999, however, the initiation year, the intensity and extent of outbreaks varied spatially and from one outbreak to another. In some instances, the occurrence of outbreaks was restricted to only one area. The general synchrony of outbreaks suggested that a large-scale extrinsic factor, such as weather, was at play. However, the imperfect synchrony of outbreaks suggested that local stand characteristics, such as canopy structure, composition of tree species and host plant quality, probably played a major role in preconditioning outbreaks. Dispersal might play a role in synchronizing outbreaks, but the extent to which it contributed to the synchrony was limited in this mountainous region.

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Spatial synchrony of population dynamics has been documented in a variety of ecological studies but the relationships to causal factors and spatial scales remain elusive (Myers 1998, Liebhold and Kamata 2000). Previous studies have addressed the link of spatial synchrony with several major ecological factors, such as environmental influence, dispersal rate, and density regulation (Lande et al. 1999, Moss et al. 2000, Ripa 2000, Williams and Liebhold 2000, Engen et al. 2002, Post and Forchhammer 2002). It seems likely that each factor plays a role in synchronizing population dynamics but their relative importance varies among animal taxa and over geographic scales.

In the study of forest insect populations, there have been increasing evidence suggesting that spatial synchrony is almost ubiquitous, especially in foliage-feeding insects (Liebhold and Kamata 2000, Peltonen 2001). In many cases it has been shown that local populations that oscillate independently due to intrinsic density-dependent processes might be synchronized by spatially correlated extrinsic factors such as large-scale climate (Royama 1984, Liebhold and Kamata 2000, Williams and Liebhold 2000). This link of spatial synchrony to regional environmental factors has been called "Moran effect" (Moran 1953), and the large-scale influence of climate has been considered broadly as a major candidate for explanation of spatial synchrony. There is no consensus, however, on the relative roles played by environmental influence and other factors such as dispersal and habitat conditions and how

they interact with each other. In the study of outbreaks of spruce budworm (*Choristoneura funiferana* Clements) in eastern North America, Sanders (1976) and Hardy et al. (1983) proposed that outbreaks originated from several epicenters and subsequently spread to other stands by dispersal. Royama (1984) considered that dispersal can enhance the size of a local population to an outbreak level, but this happens only when the population is already in an upswing phase of a cycle due to high larval survival. Williams and Liebhold (2000) used cluster analysis in their investigation of spruce budworm and suggested that outbreaks were synchronized by a combination of a spatially autocorrelated Moran effect and a high dispersal rate. It is difficult to identify the degree to which Moran effect versus dispersal regulates the spatial synchrony of animals because dispersal is very difficult to monitor in the field. Added to this controversy is the role played by heterogeneity of forest stands in affecting the spatial synchrony of outbreaks (MacLean and MacKinnon 1997, Peltonen 2001, Zhang and Alfaro 2002). Lack of long-term data on population dynamics is a major impediment to testing theories of spatial synchrony. The annual growth rings in forest trees have been recognized to contain important information about past insect outbreaks (Alfaro et al. 1982, Swetnam et al. 1985, Swetnam and Lynch 1993, Krause and Morin 1995, Zhang and Alfaro 2002). The study of tree-rings over different sites in a region can provide insights into the spatial patterns of defoliator outbreaks.

In this study, we used dendrochronological techniques to investigate the spatial patterns of two-year cycle budworm (*Choristoneura biennis* Freeman) outbreaks in central British Columbia (B.C.), Canada. This budworm, distinctive in its character of the two-year life cycle, was separated and named as a new species in the spruce budworm complex in 1967 (Freeman 1967). Moths fly in mid-July to early August, and lay their eggs immediately. Upon hatching, the young larvae overwinter in hibernacula constructed in protected places such as bark crevices. In next May to early June, the larvae emerge and feed for a brief period and enter a second diapause. In the following spring the now large larvae feed voraciously on new foliage, pupate in July and complete the two-year life cycle. This budworm is widespread in the spruce-fir forests from Prince George to Prince Rupert in B.C., and is also found in southeast Alaska, and from Jasper National Park south to the Canada-United States border (Shepherd et al. 1995). The preferred host tree species are interior spruce (*Picea engelmannii* Parry × *P. glauca* Moench) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), whereas lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) is a non-host tree species. Previous studies have shown that an outbreak of this defoliator can cause an average annual loss in radial increment from 16 to 21% (Zhang and Alfaro 2002). The characteristics and the extent to which the outbreaks occurred synchronously over different areas are, however, not well understood.

The purpose of this research was to develop tree-ring chronologies of host tree species for different areas in the Prince George region and to identify the spatial patterns of past outbreaks. The long time series of tree-ring data allowed us to analyze possible candidate factors that generate the observed tree-ring patterns and to examine whether or not a synchronizing factor operates in the same way through time and over different geographic areas.

Materials and methods

Study area and tree-ring samples

An outbreak of two-year cycle budworm has been observed in the Prince George Region of central B.C. since the late 1980s. This region is comprised of mainly two biogeoclimatic zones. The sub-boreal-spruce (SBS) biogeoclimatic zone is generally located in areas from valley bottoms to 1100–1300 m elevation, and the Engelmann spruce-subalpine fir (ESSF) zone occurs predominately in mountainous terrain at an elevation of 900 to 2100 m (Meidinger and Pojar 1991). Mean annual temperature of the SBS zone ranges from 1.7 to 5°C, and mean annual precipitation ranges from 440–900 mm; whereas the ESSF has a mean annual temperature ranging from −2 to +2°C, and a highly variable precipitation within the zone (Meidinger and Pojar 1991). The forest is dominated by interior spruce and sub-alpine fir, which are climate-perpetuated climax tree species. Lodgepole pine pioneers extensive serial stands and is common in mature forests in the drier parts of the zones (Meidinger and Pojar 1991).

In the summer of 1998 and 2000, we collected increment cores from host (spruce and sub-alpine fir) and non-host (lodgepole pine) tree species in the outbreak area of four administrative forest districts, i.e. the Fort St. James, Mackenzie, Prince George and Robson Valley Districts (Fig. 1). These tree-ring samples were collected at 39 sites in eight areas encompassing a distance of approximately 150 km from east to west and 450 km from north to south. The selection of sampling sites was based on aerial overview defoliation surveys and ground observations of defoliation. At each sampling site, one core per tree was extracted at breast height from the largest and presumably oldest trees. These cores were stored in plastic straws for transport.

Development of tree-ring chronology

In the laboratory, all increment cores were examined and a total of 568 good quality samples (e.g. old-aged
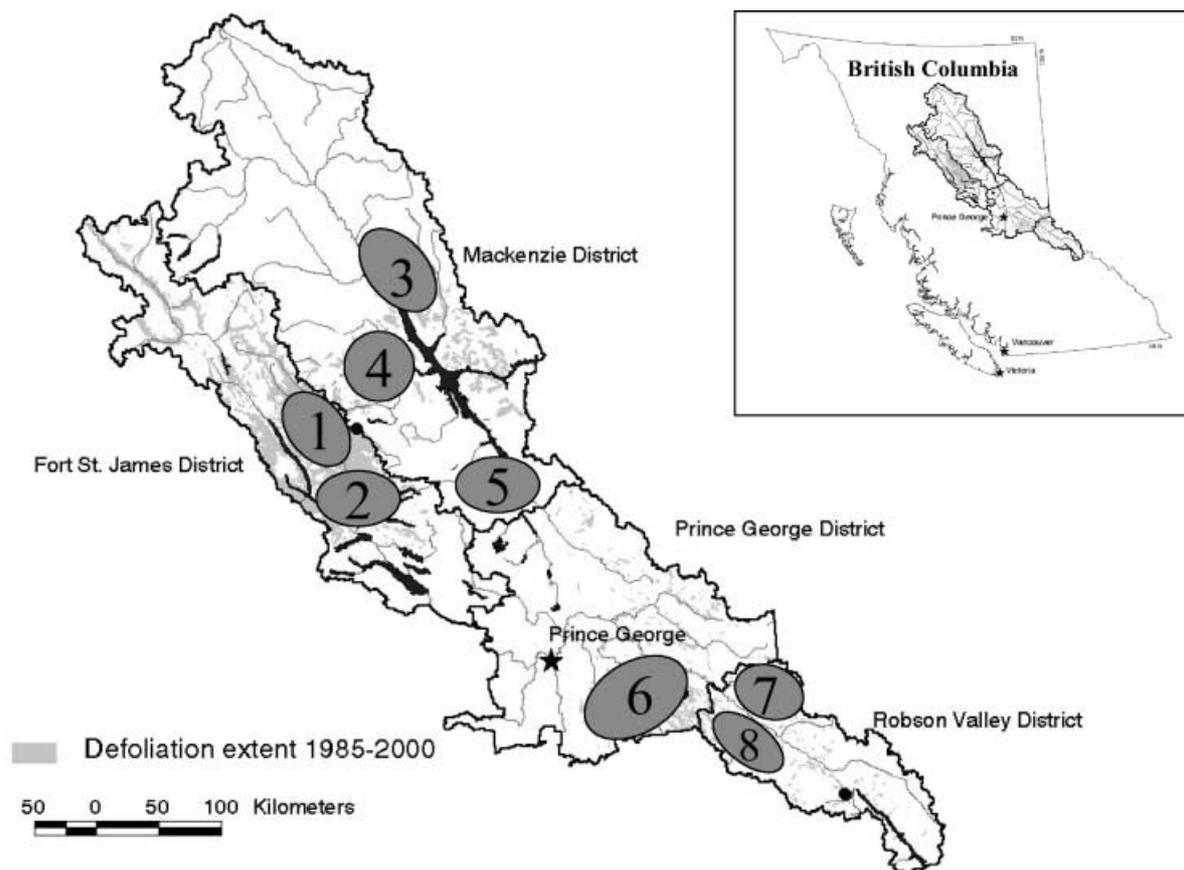
Fig. 1. Map of the study area showing the extent of two-year cycle budworm defoliation during 1985 to 2000 (shaded area) and the locations of tree-ring samples (ellipse area). 1: Germansen (F-GM), 2: Tchentlo (F-TL), 3: Ospika (M-OS), 4: Chunamon (M-CH), 5: Finlay-Philip (M-FP), 6: Bowron East (P-BE), 7: Hellroaring-McKale (R-HM), 8: Milk-Boreal (R-MB). The black parts stand for rivers or lakes.

and non-fragmented) were selected for dendrochronological analysis (Table 1). These cores were mounted on grooved wooden boards with the cross-section facing up. The sample surface was polished with progressively finer sandpapers (grits 220 to 600) to bring the ring features clearly visible. The ring widths were measured to the nearest 0.01 mm using a Windendro™ image-processing system (Régent instruments Inc., Quebec,

Table 1. Chronology length and mean inter-serial correlation for the eight areas in the Prince George Region used to study the spatial patterns of two-year cycle budworm outbreaks (at least 5 sample replications per area).

Forest district	Sampling area[1]	Sub-alpine fir		Interior spruce		Pine	
		Chronology length	Mean inter-serial correlation	Chronology length	Mean inter-serial correlation	Chronology length	Mean inter-serial correlation
Fort St. James	1) F-GM	1751–1997	0.49(24)[2]	1711–1997	0.53(28)	1696–1997	0.48 (57)
	2) F-TL	1773–1997	0.52(58)	1678–1997	0.53(81)		
Mackenzie	3) M-OS	1789–1997	0.45(52)	1799–1997	0.44(62)	1851–1997	0.44 (45)
	4) M-CH	1800–1997	0.52(19)	1792–1997	0.54(23)		
	5) M-FP	1845–1999	0.52(16)	1835–1999	0.44(18)		
Prince George	6) P-BE	1831–1999	0.55(26)	1840–1999	0.56(21)		
Robson Valley	7) R-HM	1859–1999	0.53(20)	1860–1999	0.43(13)	1880–1985 (four samples from 1985 to 1999)	0.56 (5)
	8) R-MB	1835–1999	0.55(16)	1855–1999	0.44(18)		

[1] For location, see Fig. 1.
[2] Number in brackets indicates the number of samples used in chronology building.

Canada). All the measured ring-width sequences were plotted and, with the aid of a microscope, the patterns of wide and narrow rings were cross-dated among trees of the same area to identify possible false rings, missing rings, or measurement mistakes. The quality of cross dating was examined using the program COFECHA (Holmes 1983), which provides clues for the best match in ring patterns by calculating correlation coefficients among tree-ring sequences.

The radial growth pattern in non-host pine was used to adjust the outbreak signals in host tree-ring widths. To do so, we developed ring-width chronologies of non-host pine for Fort St. James, McKenzie and Robson Valley Districts. We did not produce a chronology of pine for the Prince George District because the number of samples available was limited. The development of the three pine chronologies was conducted using the software ARSTAN (Cook and Holmes 1996) in which the measured tree-ring sequences were standardized by dividing the ring-width for each year by a fitted-curve value for that year. The fitted-curve, which represents the age-related biological growth trend, was selected as a negative exponential curve, a regression line of negative slope, or a horizontal line drawn through the mean of the series. The subsequent standardized series were then averaged together by year among different samples. The resulting yearly values, called tree-ring indices, formed the pine chronology for each District and represented the growth variation affected mainly by regional climatic factors.

Corrected ring-width chronology of host tree species was developed for each of the eight areas using the following procedures. 1) The measured host ring-width sequences were standardized in the same way as for the pine trees. 2) The standardized ring-width sequence for each sample was corrected by subtracting from it the signals not related to the budworm outbreaks. This correction was conducted using the software OUTBREAK (Holmes and Swetnam 1996), which calculated the signals not related to outbreak by the following formula:

$$(\text{Non-host index} - \text{Mean of non-host indices})$$

$$\times \frac{\text{Standard deviation of host indices}}{\text{Standard deviation of non-host indices}}$$

3) The corrected tree-ring sequences in each area were averaged by year among different samples. The resulting corrected chronology conserved the common signals due to insect defoliation in different samples while reducing the climatic signals, as well as any random signals due to micro-site influence. The length of all the chronologies used for analysis was chosen from the interval that had at least 5 sample replications.

Spatial patterns of two-year cycle budworm outbreaks

The spatial patterns of two-year cycle budworm outbreaks were examined visually and statistically by comparing tree-ring signals of outbreaks over the eight study areas. The detection of outbreaks from tree-rings was based on comparison of the growth patterns between host and non-host trees and on the characteristics of radial growth response in host trees to outbreaks. Previous studies (Zhang and Alfaro 2002) indicated that an outbreak of two-year cycle budworm would suppress the radial growth of host trees for about 10–14 years and the alternate year of feeding by the late-larval stage of budworm would create a "sawtooth" pattern in tree-rings of mid- to severe defoliated trees. Correlation coefficients among tree-ring chronologies were used to test the degree to which the tree-ring record in one area was associated with those in other areas. Tree-ring signals of outbreaks in the current period and the 1950s to early 1960s were confirmed by records from ground observations and aerial overview defoliation surveys (Unger 1984). Earlier records were not available for this region.

For each of the four forest districts, the number of host trees (including both spruce and sub-alpine fir) that showed a growth reduction greater than 1.5 standard deviations for at least four consecutive years were counted based on the corrected host tree-ring sequences. The percent of trees affected by such severe growth reduction was calculated for each year and considered to be a consequence of budworm activity. The calculation was conducted using the software OUTBREAK (Holmes and Swetnam 1996). A threshold of 40% of the trees affected was chosen as a criterion for possible outbreaks, and the patterns of peaks and troughs were examined for spatial synchrony over different districts. It was expected that extensive outbreaks would be reflected in a higher percentage of samples that had severe growth reduction. In this study, we addressed the spatial pattern of outbreak intervals rather than the annual features within an outbreak period.

Results

The tree-ring samples used to build chronologies showed significant inter-serial correlation in each study area. Mean inter-serial correlation, which describes the amount of common signal among tree-ring series of different samples, ranged from 0.43 to 0.56 for the eight study areas (Table 1). This indicated that the increment growth of individual samples responded pretty simultaneously to environmental influence (including defoliation) within each of the eight areas (Fritts and Shatz 1975). The length of chronologies for both host and
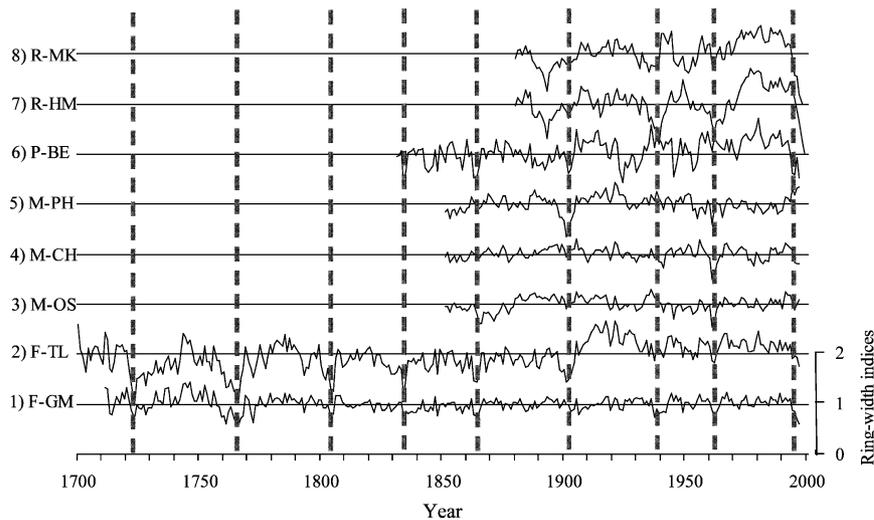
Fig. 2. Corrected ring-width chronologies of host tree species for the eight areas in Prince George Region, British Columbia, Canada. The vertical dashed lines indicate years around which possible defoliation caused significant growth reduction over a large area (for the full name of each study area, see Fig. 1).

non-host trees in the Fort St. James District was longer than that of the chronologies in other three districts, suggesting a longer stand-replacement interval and different disturbance regimes among these districts.

In each study area, the corrected chronology of spruce was compared with that of sub-alpine fir, and the result showed that the correlation coefficient ranged from 0.61–0.94 (all significant at the 99% confidence level), indicating a similar response by both species. Therefore, we did not present the chronologies of these two species separately, but rather we developed a single host chronology for each study area by averaging the chronologies from both spruce and sub-alpine fir (Fig. 2). This averaged chronology retained the common signals in the individual chronologies while reducing the signals specific to individual species.

Visual examination of the host chronologies showed that severe growth reductions occurred more or less synchronously eight times in the past 260 years in the Prince George region (Fig. 2). Since the signal of climatic influence on the growth of host trees had been minimized by the non-host chronology, the severe growth reductions were most likely caused by budworm outbreaks. Field observation of defoliation since the 1950s confirmed the outbreaks in the 1950s to early

1960s and in the 1990s (Unger 1984, Humphreys 1995). Earlier outbreaks were inferred from corrected tree-ring chronologies.

Correlation analysis of the eight host chronologies for the common interval A.D. 1880–A.D. 1997 showed that areas separated by short distances generally had higher correlation than those farther away (Table 2). For example, the chronology for area 1 was highly correlated with that of areas 2 and 4; the same occurred for the chronologies for areas 6, 7 and 8 (Table 2 and Fig. 1).

The eight outbreaks during the period A.D. 1740–A.D. 1999 were also identifiable from the calculation of percentage of trees showing periods of reduced growth attributable to defoliation. A high percentage of trees affected by defoliation occurred synchronously in Fort St. James, Prince George, and Robson Valley Districts in the 1990s, in McKenzie and Robson Valley Districts in the 1950s to early 1960s, in Fort St. James, McKenzie, and Robson Valley Districts in the late 1930s, in Fort St. James, Prince George, and Robson Valley Districts in the 1890s to early 1900s, and in Fort St. James and Prince George Districts in the 1860s (Fig. 3). The long tree-ring series for the Fort St. James District also recorded outbreak signals further back in time, i.e.,

Table 2. Correlation coefficients among the eight host chronologies in the Prince George Region in a common interval A.D. 1880–A.D. 1997. The coefficients which are significant at p<0.001 are shaded grey (for location and name of each area, please see Fig. 1).

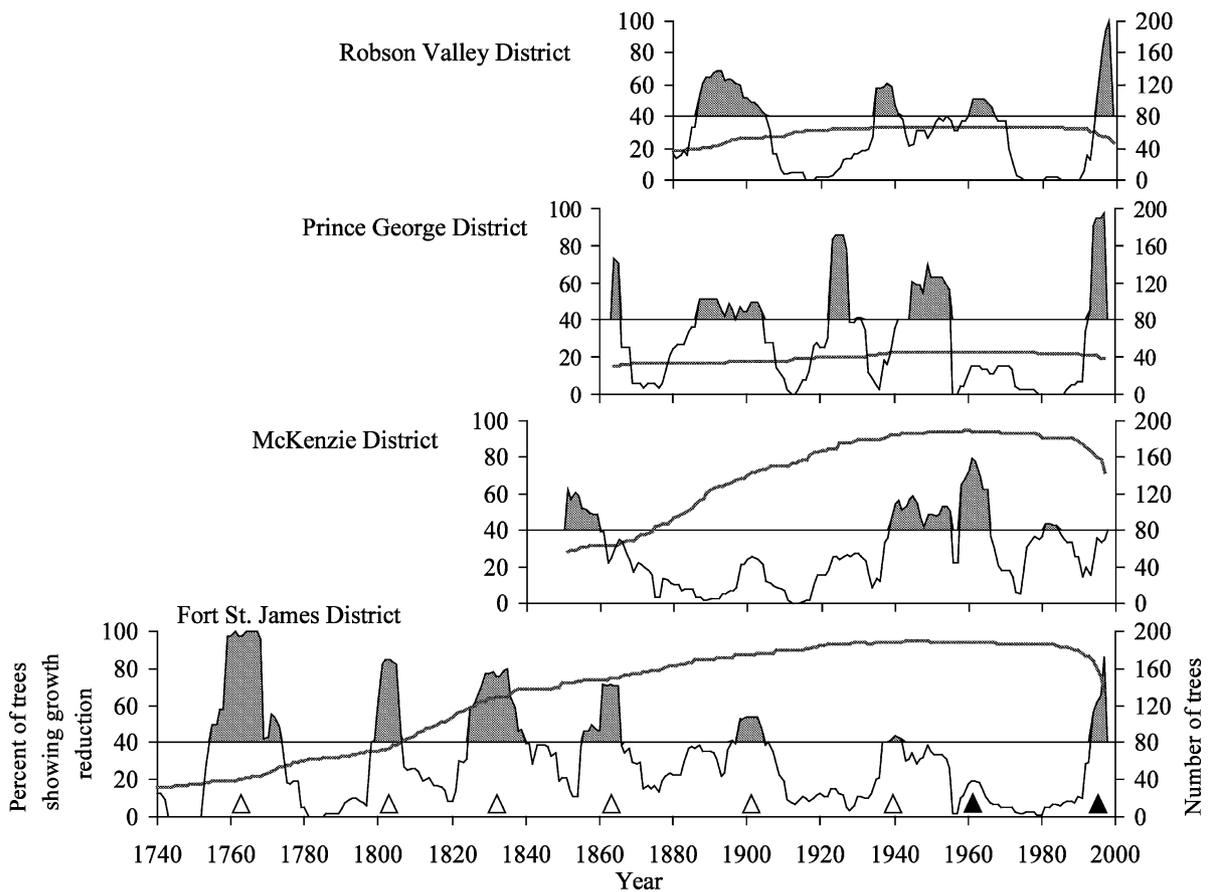|	1) F-GM	2) F-TL	3) M-OS	4) M-CH	5) M-FP	6) P-BE	7) R-HM	8) R-MB
1) F-GM	1.00							
2) F-TL	0.51	1.00						
3) M-OS	0.21	0.11	1.00					
4) M-CH	0.55	0.26	0.63	1.00				
5) M-FP	−0.04	0.47	0.41	0.25	1.00			
6) P-BE	0.26	0.44	0.22	0.10	0.09	1.00		
7) R-HM	0.28	0.27	−0.01	0.14	0.01	0.29	1.00	
8) R-MB	0.28	0.40	−0.04	0.05	−0.11	0.54	0.69	1.00

Fig. 3. Percent of host trees showing growth reduction possibly due to defoliation in the four Districts of the Prince George Region, British Columbia, Canada. The straight line represents a threshold of 40% that was chosen as a criterion for possible outbreaks. ▲, observed outbreaks; △, inferred outbreaks.

the late 1820s to 1830s, the 1800s, and the late 1750s to 1760s (Fig. 3).

A notable pattern from Fig. 3 was that, in an extensive regional outbreak, the percentage of affected-trees in some areas might not emerge above the set outbreak threshold but it would still increase to a peak relative to the adjacent periods. For example, the percentage of affected trees in the early 1960s in the Fort St. James district (outbreak no. 2 in Fig. 3) and in the late 1890s-early 1900s in the McKenzie district (corresponding to outbreak no. 4 in the Fort St. James district, Fig. 3) showed an upswing pattern although they did not reach the set level of 40%. We will discuss this phenomenon in the next section.

It was noted that variability was also apparent in the magnitudes and beginnings and ends of outbreaks from area to area, and in some instances, outbreaks occurred only in one restricted area (Fig. 3). For example, the outbreak starting in the late 1930s in the McKenzie district seemed to continue to the early 1960s, with only a short break in the mid-1950s. In the Prince George district, an outbreak occurred in the 1920s, whereas in the same period the Fort St. James and Robson Valley

districts showed a trough in the curve of percentage of affected trees and the McKenzie district showed an upswing feature. In the McKenzie district, the curve of percentage of affected-trees showed a peak slightly above the set threshold in the early 1980s whereas the other three districts showed a trough in the same period.

The high percentage of affected-trees in the Fort St. James district in the 1800s, and 1750s–1760s was obtained from only a few sampling sites. Therefore, the extent to which it represented a large outbreak is uncertain.

Discussion

In this study, we provide long time series of tree-ring data over different areas to analyze the spatial patterns of two-year cycle budworm outbreaks in the spruce-sub-alpine fir forests of central B.C. The accuracy of the tree-ring data as a proxy of the budworm activity is dependent on the sensitivity of tree rings to different

degrees of defoliation, and the cautions for interpreting tree-ring data have been discussed by Swetnam et al. (1985) and Zhang and Alfaro (2002). While a corrected mean tree-ring chronology provides an average signal of past outbreaks, the calculation of percentage of individual trees affected by defoliation provides complementary information about the extent to which a forest land is affected by outbreaks.

The spatial synchrony of two-year cycle budworm outbreaks is apparent in the corrected host tree-ring chronologies (Fig. 2) and in the percentage of trees affected by defoliation (Fig. 3). This synchrony is more evident if we take into account the minor peaks that did not emerge above the set 40% threshold. Minor peaks reflect a defoliation event that appears in fewer than 40% of the trees. Due to patchiness in defoliation during an outbreak, the degree to which the defoliation occurs in a forest stand usually differs from tree to tree (Alfaro et al. 1982). Therefore, the amplitude of outbreak signals recorded by tree rings varies among individual trees. Light defoliation has no or a minimal effect on the radial growth of trees. If an infested forest stand is less uniform in defoliation, the percent of trees that are severely attacked will be low and may not exceed the set 40% threshold. However, minor peaks in the percentage of affected trees (Fig. 3) indicate that a relatively small number of defoliated trees over a patchy forest stand may still produce an identifiable signal in the curve of percent trees affected.

Our study added evidence to a previously reported phenomenon that cyclic forest insect outbreaks tend to be spatially synchronized although the populations may not reach the same level of density in each cycle (Myers 1993, Bjørnstad 2000). The periodicity of the two-year cycle budworm outbreaks was already noted in a previous study in the Fort St. James District (Zhang and Alfaro 2002) and, as revealed in the current study, this periodic feature held true also in other districts (Fig. 2 and 3). For the spatial pattern of outbreaks, it is generally agreed that an extrinsic density-independent environmental cue operating over a large spatial scale, such as weather, plays an important role in synchronizing geographically separated population oscillations (Royama 1984, Shepherd 1985, Williams and Liebhold 1995, Myers 1998, Williams and Liebhold 2000). However, the causal mechanisms by which an extrinsic weather variable influences the spatial synchrony are poorly understood because of the difficulties in obtaining enough data about variations in both populations and their environments. Myers (1998) pointed out that identification of synchronizing signals rather than causal mechanisms may increase success in predicting patterns on a larger geographical scale.

The corrected host tree-ring chronologies developed in our study showed that, through the time, the outbreaks were synchronized in some periods but not well-synchronized in other periods. For example, in the

Robson Valley and Prince George districts, outbreaks occurred synchronously in the late 1880s to early 1900s and in the late 1990s, but the other two outbreaks in between were not in synchrony (Fig. 3). Peltonen (2001) investigated the spatiotemporal outbreak data of six forest insect species and pointed out that the Moran effect could not explain the fact that the decrease of synchrony with increasing distance was much steeper for outbreak data than for weather data. These facts suggested that factors other than weather were at play in regulating the spatial patterns of insect outbreaks.

Although dispersal is a possible candidate factor for explaining the spatial synchrony of outbreaks, we argue that its potential influence can only be realized when the physical setting and the stand characteristics are favorable for dispersal and larval development. The mountainous topography in our study region may limit the distance of dispersal. Also, closed canopy stands have been found to be less favorable to larval movement and development than open stands (Shepherd 1959, Alfaro et al. 2001). Dispersal may play a role in synchronizing outbreaks, but the existence of asynchrony over relatively close areas (as pointed in the above paragraph) suggests that dispersal is unlikely a major factor causing the synchrony of outbreaks at the regional scale. Therefore, we suspect that the contribution of dispersal to the synchrony of outbreaks varies both in space and in time for the two-year cycle budworm in our study region.

Considering the spatial and temporal characteristics of the two-year cycle budworm outbreaks, it seems that stand characteristics may be important factors influencing the occurrence and persistence of outbreaks. These stand characteristics include the features such as canopy structure, composition of tree species, and host plant quality. It has been reported that the susceptibility of forests to budworm attacks is related to the total crown area, the amount of staminate flowers of fir, and the proportion of fir in the forest (Shepherd 1959, Blais 1985, MacLean and MacKinnon 1997, Shand et al. 2001). Intense outbreaks may deplete the fir component, change the host tree quality and induce tree resistance, and subsequently reduce stand susceptibility to budworm defoliation (Underwood 1999, Alfaro et al. 2001, Awmack and Leather 2002). Since large-scale climate and geomorphologic processes usually produce spatial autocorrelation in forest characteristics (Allen and Star 1982, Tilman and Kareiva 1997), a regional outbreak could occur synchronously in susceptible stands when the weather condition favors population increase. However, even if the weather conditions are favorable, outbreaks will not occur in forests where the stand characteristics are not suitable for budworm increase (Shepherd 1959). Thus, variations in the timing and amplitudes of outbreaks are probably related to differences in the local stand dynamics. It appears that it is the combination of forest susceptibility and

weather conditions that produced the periodicity and spatial patterns of budworm outbreaks in the study region.

In conclusion, the long tree-ring records of two-year cycle budworm outbreaks showed that four outbreaks occurred more or less synchronously over the entire region in the past 120 years. It seemed that the population of two-year cycle budworm oscillated following an intrinsic mechanism, which might be related to the periodic change in stand characteristics such as stand susceptibility and host plant quality. In other words, forest characteristics may be a major factor preconditioning the outbreaks. Due to the spatial autocorrelation in forests over a large geographical area, outbreaks tended to occur synchronously in susceptible stands when the weather favored population increase, either directly by affecting the larval development and dispersal or indirectly by affecting the host tree quality. The contribution of dispersal to spatial synchrony may be limited for the two-year cycle budworm in this mountainous region. The spatiotemporal patterns of budworm outbreaks, as revealed in this study, will be useful for evaluating and forecasting the ecological impacts of defoliation on forests over the large geographical scale where the two-year cycle budworm is distributed. We recommend further research to detail the relationships between the occurrence of two-year cycle budworm outbreaks and the stand characteristics.

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