
Periodicity of Two-Year Cycle Spruce Budworm Outbreaks in Central British Columbia: A Dendro-Ecological Analysis

Qi-Bin Zhang and René I. Alfaro

ABSTRACT. An outbreak of the two-year cycle budworm (*Choristoneura biennis* Freeman) has caused defoliation damage to interior spruce (*Picea engelmannii* Parry \times *P. glauca* (Moench)) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) forests of north central British Columbia for more than 10 yr and was ongoing in 1999. A sample of 429 increment cores from spruce, subalpine fir, and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) was collected in areas of chronic defoliation, and used in a dendro-ecological study. The objective was to develop accurately dated ring-width chronologies of each species and, by comparing growth rates of the budworm host tree species (spruce and fir) with those of the nonhost pine, to determine the past history of budworm outbreaks in the region. This history would help in estimation of the potential duration and severity of the current outbreak in the region.

Four periods of decade-long reduced growth attributable to budworm defoliation were identified in the increment cores from both spruce and subalpine fir. These occurred in the mid-1890s to the early 1900s, the mid-1920s to the mid-1930s, the 1950s to the early 1960s, and the late 1980s to present (1999). Outbreaks recurred approximately every 32 yr. The reduced growth period, indicative of past outbreaks, consisted of a growth reduction phase lasting 7 to 11 yr in which rings generally exhibited a pattern of alternating wide and narrow rings (a “saw-tooth” pattern). This pattern was attributed to the biennial nature of the life cycle of this budworm, in which severe damage is caused every other year. The growth reduction phase was followed by a growth recovery phase lasting 3 to 5 yr in which ring-width gradually returned to pre-outbreak levels. Thus, the entire growth loss period could last from 10 to 16 yr and cause an average annual loss in radial increment from 16 to 21%. The 32 yr cycle of outbreak recurrence was attributed to changes in forest structure in which the forest evolves from a nonsusceptible to a susceptible state as the proportion of subalpine fir present in the upper canopy increases relative to the spruce component. A 2 yr cycle budworm outbreak will selectively remove the subalpine fir component returning the forest to a less susceptible state. It was concluded that the 2 yr cycle budworm is an important disturbance agent of northern British Columbia forests causing significant growth loss. *FOR. SCI.* 48(4):722–731.

Key Words: Insect disturbance, forest growth, tree-ring, herbivory.

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THE TWO-YEAR CYCLE SPRUCE BUDWORM (*Choristoneura biennis* Freeman) is a major insect defoliator of coniferous trees in the interior and subalpine forests in British Columbia (BC). The preferred host tree species are interior spruce (*Picea engelmannii* Parry × *P. glauca* [Moench] Voss) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). An outbreak of this defoliator has been observed in the interior of BC since the late 1980s. Assessment of the potential effects of the current outbreak on forest growth mandates a need to understand the historical pattern of the 2 yr cycle budworm outbreaks and the radial growth responses in forest trees to defoliation.

The earliest recorded outbreak of the 2 yr cycle budworm in British Columbia occurred in the Barkerville area, about 120 km southeast of Prince George, during the late 1920s to 1930s (Mathers 1932). However, there are very few studies on the long-term spatial-temporal patterns of this defoliator. Studies of a related spruce budworm (*Choristoneura fumiferana* [Clem.]) indicated that the outbreaks recurred quasi-periodically in the past few centuries, and that severe outbreaks caused topkill, reduction of growth, reduced lumber quality, and tree mortality (Blais 1983, Shore and Alfaro 1986). Given that the forests in this region are currently infested by the 2 yr cycle budworm and that there is the potential of recurrence of outbreaks in the future, knowledge of the historical patterns of outbreaks can assist managers in forest planning and implementation of contingency measures.

The purpose of this research was to determine the historic frequency and past growth impacts of the 2 yr cycle budworm on defoliated stands in the subalpine forests of central BC. We also attempted to understand the potential duration and growth impacts of the current infestation. For this, we used dendro-ecological techniques (Swetnam et al. 1985, Fritts and Swetnam 1989) to analyze a sample of increment cores of spruce, subalpine fir, and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) collected from this region in the summer of 1998. Lodgepole pine is normally not a host tree species for this budworm, although it can occasionally be defoliated during severe outbreaks if mixed with the host species. Dendro-ecological techniques have been used in the past to detect the history of insect outbreaks and to examine the tree-ring growth responses to insect-caused defoliation (Mott et al. 1957, Blais 1965, 1983, Williams 1967, Thomson and Van Sickle 1980, Alfaro et al. 1982, Krause and Morin 1995a, b, Zhang et al. 1999). The key objectives of our study were to: (1) determine the history of budworm outbreaks for the last one hundred years; (2) estimate the intensity, extent and periodicity of past budworm outbreaks; and (3) estimate potential duration and intensity of the current outbreak.

Biology and Distribution of the 2 Year Cycle Budworm

The 2 yr cycle budworm was separated and named as a new species in the spruce budworm complex in 1967 (Freeman 1967). Dang (1985) presented a key for the identification of species within the genus *Choristoneura*. Although the morphological features between *C. biennis* and other bud-

worm species such as *C. fumiferana*, *C. occidentalis*, and *C. orae* are difficult to distinguish, the character of the 2 yr life cycle is distinctive in *C. biennis* and was recognized and described as early as 1932 (Mathers 1932).

The biological characteristics of the 2 yr cycle budworm have been studied by several researchers (Shepherd 1959, 1961, Harris 1963, 1964, Campbell 1967, Freeman 1967, Freeman and Stehr 1967, Harvey 1967, Harvey and Stehr 1967, Stehr 1967, Stock and Catroville 1981, Harvey 1985a, b). The 2 yr cycle of this budworm is as follows. Moths emerge from mid-July to early August, mate, oviposit, and die in about 2 wk. Females deposit about 150 eggs in several flattened shingle-like masses on the underside of needles, which hatch within 2 wk. The newly emerged larvae do not feed but seek shelter, spin hibernacula, and overwinter as second instar larvae. Following overwintering, in late May to early June, the larvae become active, mining needles and buds for 3–4 wk, then spin hibernacula and overwinter for a second time as fourth instar larvae. Larval development is completed during the spring of the second year when the greatest amount of feeding occurs. A short pupation period in July precedes the emergence of adults.

The 2 yr cycle budworm occurs mainly in the subalpine forest region and in the adjacent section of the boreal forest (Stehr 1967, Meidinger and Pojar 1991). However, Shepherd et al. (1995) found that the geographic distribution of this budworm was more extensive than previously known. The budworm was widespread in the spruce–fir forest from Prince George to Prince Rupert in BC. It was also found in southeast Alaska, and in the Rocky Mountains, from Jasper National Park south to the Canada–United States border.

Materials and Methods

Tree-Ring Samples and Chronology Development

Our study area is located within the Fort St. James and Mackenzie Forest Districts of central BC. These two forest Districts are comprised of mainly two biogeoclimatic zones: the Sub-Boreal-Spruce (SBS) zone from the valley bottom to 1,300 m above sea level and the Engelmann Spruce-Subalpine Fir (ESSF) zone at an elevation of 900 to 1,700 m (Meidinger and Pojar 1991). The forest is dominated by interior spruce and subalpine fir, which are climate-perpetuated climax tree species. Lodgepole pine pioneers extensive seral stands and is common in mature forests in the drier parts of the zones (Meidinger and Pojar 1991).

Increment cores were collected from interior spruce, subalpine fir, and lodgepole pine trees in the Fort St. James and Mackenzie Forest Districts during June to mid-July of 1998. One core per tree was extracted at breast height from the largest and presumably oldest trees in areas that have an active budworm infestation (Bugbusters Pest Management Inc. 1999). In total, 793 cores were collected from 98 stands (about 8 cores per stand) in the Fort St. James Forest District, and 540 cores were collected from 69 stands in the Mackenzie Forest District.

In the laboratory, all increment cores were examined and those of good quality (e.g., old-aged, having sensitive rings, nonfragmented, and free from rot), were selected for dendro-

ecological analysis. A total of 429 cores (228 from the Fort St. James Forest District and 201 from the Mackenzie Forest District) were selected and used in the tree-ring analysis (Table 1). The selected samples were then mounted into slotted wooden boards and polished with progressively finer sandpaper (grits 220 to 600) to enhance the boundaries between the annual rings.

The ring-width measurement was conducted using a Windendro™ tree-ring image processing system. The precision of the measurement was 0.01 mm. All the measured ring-width sequences were plotted, and the patterns of wide and narrow rings were cross-dated among trees to identify possible false rings, missing rings, or measurement mistakes. The increment cores with very narrow rings were also examined under a microscope to ensure that each ring was assigned with a correct calendar year of ring formation. The quality of cross-dating was examined using the program COFECHA (Holmes 1983), which provides clues of the best match for ring patterns by calculating correlation coefficients among tree-ring sequences. The age-related growth trend within each ring-sequence was removed using the program ARSTAN (Grissino-Mayer et al. 1993) in which the detrending curve selected was either a negative exponential curve, a regression line of negative slope, or a horizontal line drawn through the mean of the series. Deviations from this curve were standardized to produce a set of annual growth indices for each sample. Ring-width chronology for each species was derived by averaging the growth indices for each year among different trees for the study area (Fritts 1976). The resulting yearly values in the chronology, called ring-width indices, represent the growth variations affected by macro-environmental factors. The length of all the chronologies used for analysis was chosen from the interval that had at least ten sample replications.

Detection of the 2 Year Cycle Spruce Budworm Outbreaks from Tree Rings

The detection of 2 yr cycle budworm outbreaks from tree rings was based on the pattern of the radial growth response to field-observed defoliation and on comparisons with the growth response of pine, a nonhost tree species for the budworm, in the same period. Budworm activity in this region was recorded by field and aerial observers of the Canadian Forest Service, Forest Insect and Disease Survey (FIDS) for the period after 1948. Major defoliation was observed for two periods, the 1950s to the early 1960s and the late 1980s to present (1999). Earlier records were not available for this region. Based on studies of the growth response of forest trees to other insects, e.g., western spruce budworm (*Choristoneura occidentalis* Freeman) (Alfaro et al. 1982,

Swetnam and Lynch 1993, Weber and Schweingruber 1995), it was expected that the radial growth of host trees would be reduced significantly and that the suppression would last for several years. We also expected that there would be an alternate growth rhythm in tree-rings, i.e., a “saw-tooth” effect, due to the alternate years of feeding by the late-larval stage of the budworm. However, the response of tree rings to 2 yr cycle budworm has not been measured before.

Growth changes (GCH) from one year to the next were calculated for each sampled tree using the International Tree-Ring Data Bank (ITRDB) computer software LRM (List Ring Measurement) (Grissino-Mayer et al. 1993), which used the following equation:

$$GCH = \frac{2 \times (r_t - r_{t-1})}{(r_t + r_{t-1})} \times 100\%$$

where r_t refers to the ring-width in year t ; and r_{t-1} refers to the ring width in year $t - 1$.

A negative growth change (GCH) of greater than 20% was considered as an abrupt growth reduction and a severe deviation from the natural growth trend. An outbreak of 2 yr cycle budworm would cause growth reduction only in the host species, whereas adverse climate conditions would suppress growth in both host and nonhost trees. Thus, the outbreaks could be identified by comparing growth response between host and nonhost species, by examining the percentage of trees having severe growth reduction, and by examining if the growth reduction period in host trees exhibits the year-to-year “saw-tooth” pattern in ring-widths.

Patterns of Past 2 Year Cycle Budworm Outbreaks

The duration, intensity, extent and periodicity of past 2 yr cycle budworm outbreaks were estimated by examining the yearly growth changes in each sample tree and the ring-width chronologies of each species.

The duration of outbreaks was determined by counting the number of years, from when ring-width indices started to decrease to the year of lowest indices, during an infestation. The recovery period was counted from the year of increasing ring-width indices to the year having an index value similar to the pre-infestation ring-width indices. This growth decrease and recovery period is referred to here as an outbreak-recovery period (Alfaro et al. 1982).

The amplitude of growth change in severe defoliation years and the growth loss for the whole outbreak-recovery period were used as indicators of outbreak intensity. The percent of trees that have a growth reduction rate greater than 40% was calculated for severe defoliation years. The budworm-induced growth loss (GL), relative to the growth before outbreak, was calculated as follows:

Table 1. Number of samples in four study areas used for development of tree-ring chronologies and analysis of the patterns of past 2 yr cycle budworm outbreaks in British Columbia, Canada.

Forest district	Study area	Spruce	Subalpine fir	Pine	Total
Fort St. James	Fort St. James	67	52	50	169
	Germansen-Osilinka	28	24	7	59
Mackenzie	Ospika	62	52	36	150
	Chunamon-Raspberry	23	19	9	51
Total		180	147	102	429

$$GL = \left(\frac{\bar{I}_{\text{host-outbreak}}}{\bar{I}_{\text{host-preoutbreak}}} - \frac{\bar{I}_{\text{nonhost-outbreak}}}{\bar{I}_{\text{nonhost-preoutbreak}}} \right) \times 100\%$$

where, $\bar{I}_{\text{host-outbreak}}$ and $\bar{I}_{\text{host-preoutbreak}}$ are the means of ring-width indices for host species in the outbreak-recovery period and in the 5 yr period before outbreak, respectively; and $\bar{I}_{\text{nonhost-outbreak}}$ and $\bar{I}_{\text{nonhost-preoutbreak}}$ are the means of ring-width indices for nonhost species in the outbreak-recovery period and in the 5 yr period before the outbreak, respectively. Since the GL is calculated from tree-ring indices, it is a relative measure of the growth loss.

The spatial extent of outbreaks was estimated from the percent of trees showing abrupt growth reduction during an actual (documented) or suspected infestation period. It was expected that extensive outbreaks would be reflected in a higher percentage of samples having an abrupt growth reduction than less extensive outbreaks.

Outbreak periodicity was evaluated by examining the intervals between adjacent outbreaks, which was counted as the length between the first year of two consecutive outbreaks. Spectral analysis (Statistica 1991) of the time-series of the percentage trees with abrupt growth reduction was also used to determine the outbreak periodicity.

Results and Discussion

Ring-Width Chronologies

The tree-ring samples were distributed in an area encompassing a distance of approximately 110 km from east to west and 220 km from north to south. Based on the geographic location of the core samples, four separate ring-width chro-

nologies of spruce and subalpine fir were developed for the Fort St. James and Germansen-Osilinka study areas in the Fort St. James Forest District, and for the Ospika and Chunamon-Raspberry areas in the Mackenzie Forest District, respectively (Figure 1). For each Forest District, a chronology of nonhost species (pine) was also developed (Figure 1).

The statistical descriptions of each chronology are presented in Table 2. The tree-rings of all sampled species were sensitive to environmental factors as indicated by the mean sensitivity, which measures the ring-width variability between successive years. The mean serial correlation for each chronology, which describes the amount of common signal among tree-ring series of different samples, ranged from 0.44 to 0.55. This indicated that rings from these areas responded simultaneously to large-scale climatic or biotic disturbances. The spruce and subalpine fir trees in the Fort St. James District were older, originating between the 1730s and 1790s, whereas the stands in the Mackenzie District originated in the 1850s. This age difference indicated that there might have been different disturbance regimes between the two districts.

Effect of 2 Year Cycle Budworm Outbreaks on Tree-Ring Growth

Two outbreaks have been documented in this region, one in the 1950s to the early 1960s (termed the 1950s outbreak), and the other in 1985 to the present (1999) (termed the current outbreak) (Unger 1984, Bugbusters Pest Management Inc. 1999). In both outbreaks, the defoliation was more severe in the Fort St. James Forest District than in the Mackenzie District. These two outbreaks caused the expected "sawtooth" pattern of alternating narrow and wide rings in many defoli-

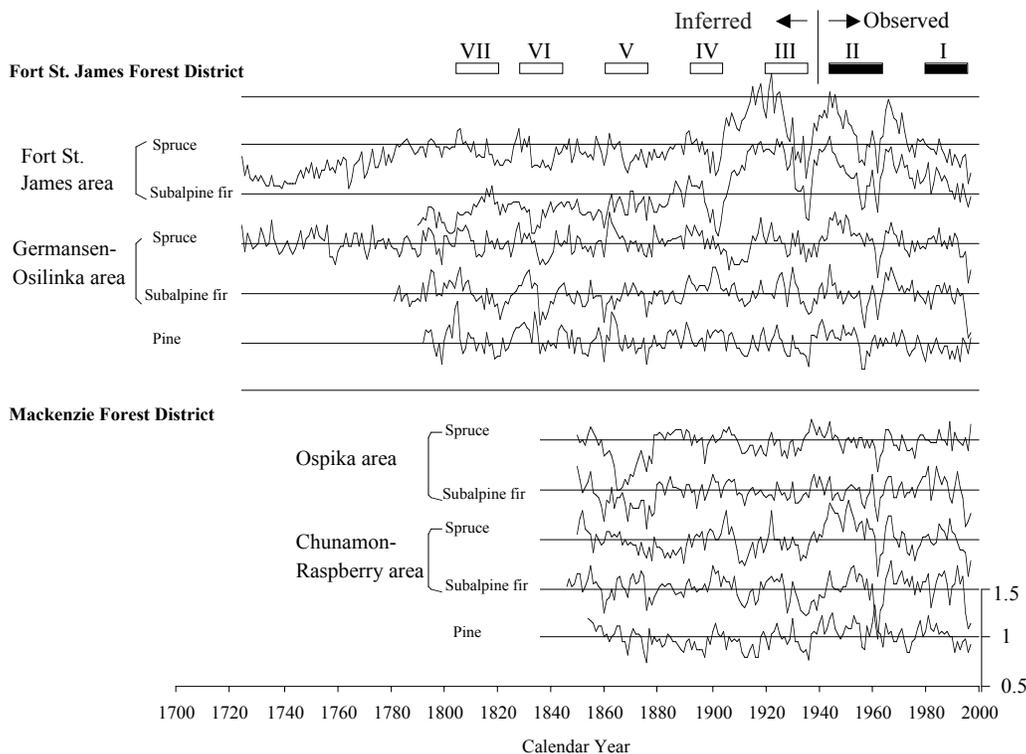


Figure 1. Ring-width chronologies of spruce, subalpine fir, and pine for the Fort St. James and Mackenzie Forest Districts in British Columbia, Canada (A.D. 1720–1997). The horizontal bars above the chronologies represent intervals of observed or inferred outbreaks.

Table 2. Chronology characteristics for spruce, subalpine fir and lodgepole pine in four study areas in British Columbia, Canada.

Forest District	Study area	Species	No. of trees	Chronology length (yr)	Mean ring-widths (mm)	Mean serial correlation	Mean sensitivity
Fort. St. James	Fort St. James	Spruce	67	278 (1720–1997)	0.98	0.55	0.19
		Subalpine fir	52	208 (1790–1997)	1.04	0.52	0.20
	Germansen-Osilinka	Spruce	28	275 (1723–1997)	0.74	0.53	0.16
		Subalpine fir	24	217 (1781–1997)	0.64	0.50	0.17
		Pine	57	206 (1792–1997)	0.96	0.48	0.18
		Spruce	62	148 (1850–1997)	1.37	0.44	0.17
Mackenzie	Ospika	Subalpine fir	52	148 (1850–1997)	1.24	0.45	0.18
		Spruce	23	148 (1850–1997)	0.98	0.54	0.16
	Chunamon-Raspberry	Subalpine fir	19	152 (1846–1997)	0.73	0.52	0.17
		Pine	45	144 (1854–1997)	1.10	0.44	0.17
		Spruce	67	278 (1720–1997)	0.98	0.55	0.19
		Subalpine fir	52	208 (1790–1997)	1.04	0.52	0.20

ated trees, although the relative changes in ring-widths varied from tree to tree. Several examples of such a “sawtooth” pattern are shown in Figure 2. Such a “sawtooth” pattern was not evident in nonhost trees.

During the 1950s outbreak, the main feeding by mature larvae occurred in the even-numbered years, e.g., 1954, 1956, 1958, and 1960. The ring widths of the budworm host species, however, did not decrease in the year of feeding but 1 yr later, e.g., 1957, 1959, and 1961 (Figure 2a). In 1961, more than 40% of the host trees in the Fort St. James Forest District reduced the increment growth by 20% relative to the growth in the previous year, whereas only 5% of the nonhost trees had such growth reduction. In 1962, a larger number of both host and nonhost trees showed a growth reduction. The climatic record in the Fort St. James weather station, about 110 km northwest of Prince George, showed that the total precipitation in July of 1962 was extremely low (5 mm versus 40 mm average), suggesting that severe water stress may have been a factor contributing to the growth reduction in both host and nonhost trees. Since the infestation collapsed in

1963 (Humphreys 1995), it is possible that the adverse weather in 1962 also played a role in reducing insect activity.

From 1985 to 1997 during the current outbreak, budworm feeding occurred mainly in odd-numbered years, and a typical “saw-tooth” pattern with narrow rings in even-numbered years was observed in many defoliated trees (Figure 2d). Extensive defoliation was observed in 1995 and, particularly, in 1997 when 400,000 ha were infested (Bugbusters Pest Management Inc. 1999). The ring-width of spruce and subalpine fir decreased dramatically in the year following the defoliation. In 1996, 76% of the spruce trees in the Fort St. James area and 46% of the spruce trees in the Ospika area reduced the increment growth by 20% relative to the growth in the previous year. Tree rings for 1998 were not present in increment cores collected in this study (since the samples were collected in the early summer of 1998), but we expected that radial growth in defoliated trees was minimal for 1998. No further statistics were conducted for subalpine fir due to the small sample size, but our observation showed that the pattern of growth reduction in subalpine fir was similar to that of spruce.

In summary, the response of tree-ring growth to observed defoliation suggested that: (1) 2 yr cycle budworm outbreaks caused growth reduction in the 1950s and in the current infestation; (2) a one year lag existed between defoliation and its effect on tree-rings; and (3) an alternating pattern of narrow and wide rings (“saw-tooth” pattern) is characteristic of 2-year cycle budworm infestation.

Previous Outbreaks in the Fort St. James Forest District in the Last 100 Years

The “sawtooth” pattern in ring-width sequences of host trees was evident in several earlier growth reduction periods (Figures 1, 2b, 2c), but this pattern was not observed in the nonhost trees for the same intervals. This alternate growth pattern occurred synchronously in many samples and confirmed the 2 yr cycle nature of the damage, although the magnitude of the damage varied from tree to tree.

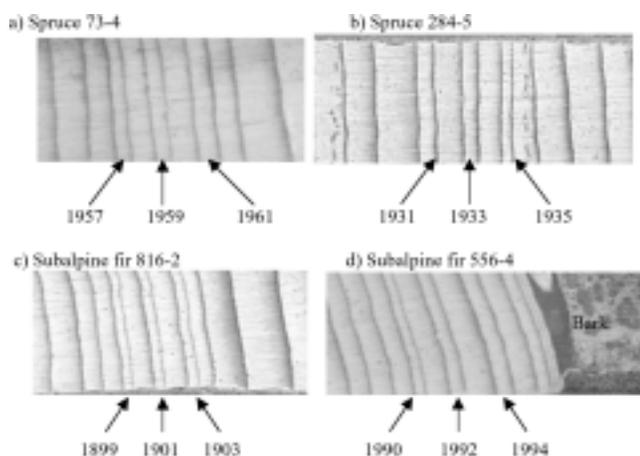


Figure 2. Examples of spruce (a and b) and subalpine fir (c and d) tree rings with alternate narrow and wide growth rhythm (a “sawtooth” pattern) caused by 2 yr cycle budworm in each of the four outbreaks in British Columbia, Canada.

Table 3. Two-year cycle budworm outbreaks in the last 100 yr in the Fort St. James area of British Columbia, Canada, reconstructed from tree-ring chronologies of spruce and lodgepole pine (a nonhost for budworm).

Outbreak no.	Years of outbreak*	Years of recovery	Growth loss (%)	Severe defoliation years*	No. of samples	Percentage of trees that have a growth reduction rate	
						≥ 20%	≥ 40%
1	7 (1894–1900)	3 (1902–1904)	19.9	1896	65	48	25
				1898	65	60	48
				1900	65	68	35
				1930	67	81	52
2	9 (1926–1934)	5 (1936–1940)	20.9	1932	67	43	19
				1934	67	91	69
				1954	67	66	28
				1960	66	41	14
3	11 (1950–1960)	3 (1962–1964)	15.6	1989	65	54	20
				1995	58	76	53
				> 8 (1989–1997) (ongoing in 1999)	> 14.8		

* The years have been adjusted for the 1 yr lag effect between defoliation and radial growth reduction.

The ring-width chronologies and growth response patterns in host and nonhost species suggests that 2 yr cycle budworm outbreaks occurred four times in the Fort St. James area during the last 100 yr (Table 3). The current and the 1950s outbreaks were documented by the Forest Insect and Disease Survey of Canada. Earlier records are not available, and the outbreaks in 1927–1935 and 1895–1901 were inferred from tree rings. The first three outbreaks lasted about 7 to 11 yr, and radial growth recovered to pre-outbreak levels in about 3 to 5 yr (Table 3). Average growth loss per year for the three outbreaks ranged from 15.6%–20.9%. After adjusting for the 1 yr lag effect on radial growth response, we concluded that severe defoliation in this area occurred in even-numbered years in the previous three outbreaks and in odd-numbered years in the current outbreak. The most severe outbreak occurred in the 1930s, and defoliation in 1934 resulted in a growth reduction rate $\geq 40\%$ in 69% of spruce trees (Table 3).

The intervals between the adjacent outbreaks in the past century were 32, 24, and 39 yr respectively (with an average of 32 yr). Spectral analysis of the time series of the percentage trees having abrupt growth reduction in the period 1870–1997 showed that two peaks occurred around 2 and 32 yr cycles (Figure 3). The 2 yr cycle is attributed to the 2 yr nature of budworm feeding activity, and the 32 yr cycle might reflect the internal and/or external factors controlling the long-term budworm population dynamics. We hypothesize that a large proportion of fir trees in the stands increases stand vulnerability to budworm damage. Since fir is more susceptible to defoliation and the mortality in a mixed spruce-fir stand is related to the proportion of the preferred host trees (MacLean and MacKinnon 1997), the elimination of the most susceptible hosts will reduce forest susceptibility and contribute to the collapse of the outbreak. It may take an average of 32 yr for the surviving fir trees in the lower canopy to reach sizes that render the forest susceptible again.

An interesting feature of the chronologies for the Fort St. James area is that the amplitude of spruce and subalpine fir chronologies was larger in the 20th century than that of the previous centuries (Figure 1, top two chronologies), but no such amplitude change was observed for the nonhost lodgepole pine. This phenomenon suggests that forest structure (e.g., tree age, composition, and density)

or environmental factors controlling spruce and fir growth might have changed in the end of the 19th century. Tree age is not likely a factor producing the differential growth response in host trees because tree-ring indices were obtained by averaging standardized ring widths from trees of different ages, and the radial growth following budworm outbreaks before the end of 19th century did not show strong release. Since there is no record of other environmental factors having such abrupt changes at the end of the 19th century, we hypothesize that outbreaks were more intense in this area during the 20th century, and that recovery after defoliation was also stronger due to thinning effects.

The spatial and temporal patterns of 2 yr cycle budworm outbreaks in the Germansen-Osilinka area in the last

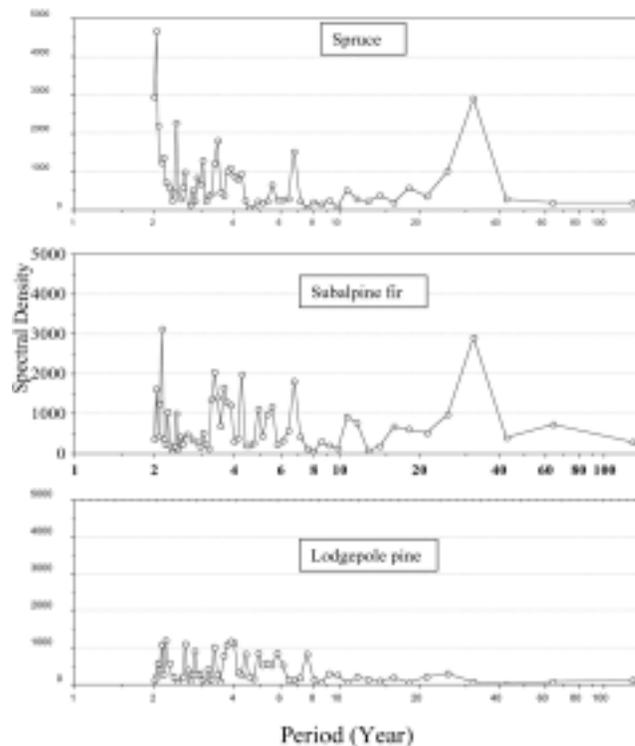


Figure 3. Spectral analysis of growth reduction in interior spruce, subalpine fir, and lodgepole pine in the Fort St. James area, British Columbia, Canada. The time series used for analysis was the percent of trees having abrupt growth reduction in the interval 1870–1997.

100 yr was similar to that in the Fort St. James area, i.e., four outbreaks were also noted since the 1900s in the tree-ring chronologies of spruce and subalpine fir (Figure 1). However, the budworm-induced changes in host tree-ring indices in this area had smaller amplitude than that in the Fort St. James area. This suggests that outbreaks and recovery periods have been less intense in this area relative to the Fort St. James area. The sampled stands in the Germansen-Oslinka area mainly belong to the moist cool subzone of the Sub-Boreal-Spruce biogeoclimatic zone (SBSwk3), whereas the sampled stands in the Fort St. James area mainly belong to the wet cool subzone of the SBS biogeoclimatic zone (SBSmk1). It has been reported that the most extensive and repeated defoliation occurred in the SBSwk3 subzone (Shand et al. 2001). Therefore, our observed spatial patterns of tree-ring chronologies are probably related to the differences in forest structure and climate between the two areas. No further statistics of the outbreaks were conducted for the Germansen-Oslinka area because the small sample size for each species made it difficult to produce any sound statistical inferences.

Outbreak History in the Mackenzie Forest District

The tree-ring chronologies of host trees in the Mackenzie Forest District (Figure 1) showed that, although outbreaks were present, they did not exhibit clear patterns of widespread, decade-long growth reduction, as seen in the Fort St. James chronologies. This suggests that the regional outbreak pattern in this district is different from that of the Fort St. James pattern. Examination of the individual cores showed that the radial growth patterns differed among the sampled stands, although they did cross-date statistically (see the mean serial correlation in Table 2). This suggests that the outbreaks tended to be light and less uniform in this district, which is consistent with the defoliation record from the FIDS aerial survey since 1948 (Unger 1984). Therefore, a better reconstruction of the outbreak history in this district might be obtained by examining the ring patterns for individual stands or groups of stands with similar characteristics.

Examination of the increment cores in selected stands showed that outbreaks occurred around the 1900s, 1930s, 1950s, and in the 1990s, similar to the Fort St. James Forest District. However, the initial year of outbreak and the degree of defoliation differed from stand to stand. For example, an outbreak probably occurred in the mid-1920s to early 1930s in stand No. 169 but not (or not so severe) in stands No. 145 and 12 (Figures 4a, c). The 1950s outbreak initiated in the late 1940s in stand No. 145, in early 1950s in stand No. 169, and in the late 1950s in stand No. 12 (Figure 4). This suggests that the outbreak started in a few restricted stands and then spread to other vulnerable stands, resulting in patchy defoliation in this mountainous region. The budworm population dynamics and the susceptibility of forests were related to stand characteristics, for example, more open stands were found to favor larval movement and development (Shepherd 1959). Studies of stand susceptibility to defoliation by eastern spruce budworm also showed that open stands were more susceptible to budworm attack than closed stands (Alfaro et al. 1999).

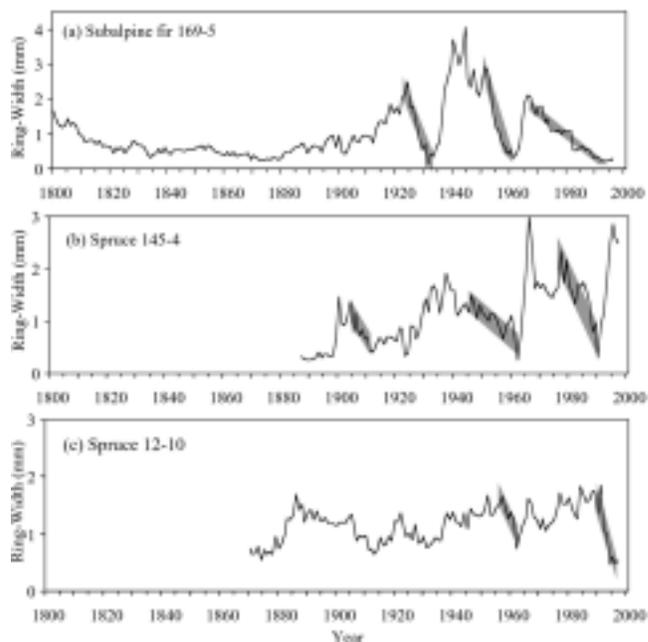


Figure 4. Examples of spruce and subalpine fir trees showing intervals of growth reductions (shaded) caused by 2 yr cycle budworm outbreaks in the Ospika area, Mackenzie Forest District, British Columbia, Canada.

Assessment of Budworm-Induced Growth Losses

We used dendro-ecological techniques to determine the patterns of past 2 yr cycle budworm outbreaks. The resulting record increases our understanding of past outbreaks with respect to duration, severity, and frequency, and enhances our ability to manage current and future outbreaks.

Radial growth of a tree is affected by a complex of environmental factors which include large-scale climate, insect infestation, microclimate, competition among trees, and others (Fritts 1976). Tree-ring chronologies, developed by averaging ring sequences from a region, emphasize the growth patterns common to all trees and cancel out differences in radial growth among different trees. Sample replication is critical in removing the effects of local environmental factors on tree growth. In our study, the sample size is the largest for the last 100 yr, and decreases in the early part of the chronologies due to the small number of available old-aged trees. Therefore, the last 100 yr of the chronologies contained more reliable information than the earlier years and were used for inferences of budworm outbreaks. If the outbreaks are spatially less uniform, such as in the Mackenzie Forest District, a large number of samples should be collected on susceptible stands and tree-ring chronologies should be developed for stands of similar characteristics.

The increment core samples used in development of the tree-ring chronologies in this study were obtained only from living trees. Severe budworm defoliation can also cause tree mortality (Unger 1984). So, the losses calculated from tree-ring chronologies may be underestimated because they include only losses of growth and not losses due to mortality. In addition, increment cores were extracted at breast height, which may further underestimate

the losses since budworm-induced growth reduction might be greater in the upper levels of the stem, as found in studies of the impact of spruce budworm defoliation on Douglas-fir (Williams 1967, Thomson and Van Sickle 1980, Alfaro et al. 1985). The complete effect of 2 yr cycle budworm on radial growth along the tree boles could be determined by examination of tree-ring samples at different levels along the stem. Radial growth reduction occurred 1 yr after the defoliation, suggesting that the stored photosynthates from the previous year play a key role in the cambial activity at breast height in a given year. A similar 1 yr lag effect was described for Douglas-fir defoliated by western spruce budworm (Alfaro et al. 1982).

Growth in nonhost trees was used to correct for climatic effects on host trees and to isolate the effects of budworm. The alternate growth rhythm observed in spruce and subalpine fir trees during an infestation was in contrast with the growth patterns in nonhost trees, suggesting that the alternate growth rhythm is not caused by large-scale climatic factor. Krause and Morin (1995b) reported that the number of latewood tracheids showed a reduction 1 yr earlier than the ring widths and this reduction might serve as an indicator of the onset of budworm defoliation. In this study, however, no obvious patterns for the growth of earlywood and latewood were found in our samples, and the reduction of the ring-widths was pronounced during outbreak periods. Since there is no record of alternate rhythm for other growth controlling factors, e.g., spraying insecticides every other year, we conclude that the "tooth-like" pattern in tree rings of spruce and balsam in this region is a result of infestation by the 2 yr cycle budworm. The degree of the alternate growth rhythm, however, varies from tree to tree depending on variation in defoliation severity and conditions of local environment. For example, if the defoliation is severe in one tree and light in an adjacent tree, the growth recovery following the reduction will be greater in the lightly defoliated tree than in the severely defoliated tree (Alfaro et al. 1982). Nevertheless, if the alternate growth rhythm shows up in quite a few host trees but not in nonhost trees, it is most likely that such growth rhythm is caused by defoliation of the 2 yr cycle budworm.

Recurrence of Outbreaks

The recurrent pattern of outbreaks of the 2 yr cycle budworm (periodicity of about 32 yr) is similar to that of eastern spruce budworm which has a cycle with periods of 30-35 yr (Royama 1984, Régnière and Lysyk 1995). This similarity suggests that the cyclic patterns may have a common explanation. The existing hypothesis for the cyclicity of outbreaks include regulations by parasitoids, pathogen, or virus (Royama 1984, Régnière and Lysyk 1995), by climatic factors (Shepherd 1985, Thomson 1985, Myers 1993), and by the susceptibility of forest to budworm attacks (Blais 1985, Alfaro et al. 1999). Although many factors could be related to the population dynamics, the cyclicity of 2 yr cycle budworm outbreaks in our study region is most likely due to a periodic change in forest susceptibility to budworm attacks. The underlying mechanism for an increase in susceptibility may be associated with increasing proportion of subalpine fir in the forest and that budworm may have a better survival and

overall fitness when feeding on subalpine fir than on spruce. Intense outbreaks may deplete the fir component and reduce stand susceptibility to budworm defoliation. Superimposed on this oscillation in forest susceptibility is the variation of year-by-year weather conditions which may play a role in synchronizing the regional outbreaks (Moran 1953, Williams and Liebhold 2000). It appears that it is the combination of forest susceptibility and weather conditions that produced the cyclicity and spatial synchrony of budworm outbreaks as shown in the host tree-ring chronologies in the two forest districts (Figure 1). The nonhost pine chronology shows apparent growth dips which coincide with the end of outbreaks II and III in the Fort St. James District (Figure 1), suggesting that unusual weather causing the growth reduction in pine might also disrupt the cycle of the budworm and cause the population to collapse.

Given the recurrent nature of the 2 yr cycle budworm outbreaks in this region, it is pertinent to ask how much longer the current outbreak will last in the Fort St. James and Mackenzie Forest Districts. Effects on growth caused by the current defoliation are clearly visible in the chronologies for spruce and subalpine fir (Figure 1). Growth declined for above 12 yr since the current outbreak began in 1985, which is longer than previous durations (Table 3). Therefore, if this outbreak is determined by the same factors as previous outbreaks and the vulnerability of trees has not changed, we would expect the last year of heavy feeding should be 1999 or 2001. A period of recovery of ring widths to pre-outbreak levels should last 3 to 5 yr. Past outbreaks are less uniform and of shorter duration in the Mackenzie Forest District, suggesting that the duration will vary from stand to stand.

Conclusion

Our study found that: (1) 2 yr cycle budworm outbreaks can cause radial growth reduction of 16–21% per year on average in spruce and subalpine fir, and the reduction at dbh occurs 1 yr after the defoliation, (2) "sawtooth" pattern in radial growth during a decade-long growth reduction period is a typical growth response of spruce and subalpine fir to 2 yr cycle budworm outbreaks, (3) four outbreaks (the mid-1890s to the early 1900s, the mid 1920s to the mid-1930s, the 1950s to the early 1960s, and the late-1980s to present) were identified in the last 104 yr (1894–1997), and these outbreaks occurred somewhat periodically every 24–39 yr and lasted 7–11 yr, followed by a recovery period of 3–5 yr, (4) in the Fort St. James area, the intensity of outbreaks increased in this century, but the frequency remained the same, and (5) outbreaks of the 2 yr cycle budworm were light and less uniform in the Mackenzie Forest District in the past century.

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