

Multicentury history of western spruce budworm outbreaks in interior Douglas-fir forests near Kamloops, British Columbia

Rochelle Campbell, Dan J. Smith, and André Arsenault

Abstract: Western spruce budworm (*Choristoneura occidentalis* Freeman) is a native defoliator of forests in the interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) forests of British Columbia, Canada. Dendrochronological techniques and the software program OUTBREAK were used to reconstruct a defoliation history of Douglas-fir for 19 forest sites near Kamloops in central British Columbia. By comparing the radial-growth response of ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws. & C. Laws.) with that of Douglas-fir growing in nearby but separate stands, eight western spruce budworm outbreaks over the past 300 years were distinguished. Although there is considerable variation in the timing and duration of these western spruce budworm events at the stand level, synchronous outbreaks have occurred in approximately 30- to 43-year cycles. Spectral analyses of a composite time series from all stands showed similar and consistent intervals between outbreaks. Climatic variation appears to have been important to budworm outbreaks in the 20th century. Notable outbreaks tended to occur during years with average spring air temperatures following winters with less than average precipitation. Based on this finding, it is proposed that with high over-winter survival rates and a longer growing season, the duration of outbreaks may increase in the future.

Résumé : La tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) est un insecte défoliateur indigène des forêts intérieures de douglas de Menzies bleu (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) en Colombie-Britannique, au Canada. Cette étude utilise les techniques dendrochronologiques et le programme informatique OUTBREAK pour reconstituer l'historique de la défoliation du douglas de Menzies bleu dans 29 stations forestières situées près de Kamloops dans le centre de la Colombie-Britannique. En comparant la croissance radiale des tiges de pin ponderosa (*Pinus ponderosa* Dougl. ex P. Laws. & C. Laws.) à celle des tiges de douglas de Menzies bleu croissant dans des peuplements voisins mais séparés, huit épidémies de la tordeuse occidentale ont été identifiées au cours des 300 dernières années. Bien qu'il y ait une importante variation dans le moment et la durée de ces épidémies à l'échelle du peuplement, des épidémies synchrones sont survenues avec une périodicité d'environ 30 à 43 ans. Les analyses spectrales de séries temporelles composées de tous les peuplements ont montré qu'il y avait des intervalles réguliers consistants entre les épidémies. Les variations climatiques semblent avoir eu un impact important sur les épidémies de tordeuse au 20^e siècle. Les épidémies les plus importantes ont eu tendance à survenir durant les années où la température de l'air au printemps était dans la moyenne après un hiver où les précipitations avaient été plus faibles que la moyenne. Sur la base de ces résultats, nous croyons qu'avec un taux de survie élevé pendant l'hiver et une saison de croissance plus longue, la durée des futures épidémies pourrait être plus longue.

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Introduction

Episodic infestations of western spruce budworm (*Choristoneura occidentalis* Freeman) (Lepidoptera: Tortricidae) in British Columbia have been reported since the early 1900s and have caused widespread defoliation that

has lasted from a few to 10 or more years (Brubaker and Greene 1979; Harris et al. 1985). Severe historical western spruce budworm infestations appear to be related to warm dry summers, when optimal synchrony between larval emergence and bud flush increases the vulnerability of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) trees to attack by the western spruce budworm (Thomson et al. 1984). It is predicted that impending climatic changes within interior British Columbia will lead to increasingly warmer and drier summers (Columbia Mountains Institute of Applied Ecology 2005) that are anticipated to increase the severity and frequency of significant western spruce budworm infestations over the next century (Williams and Liebhold 2000).

Across North America, episodic outbreaks of defoliating insects of the genus *Choristoneura* have stimulated research aimed at understanding their biology and impact (Mason et al. 1997; Parent et al. 2001). In the Interior Douglas-fir For-

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est (IDF) zone of British Columbia, western spruce budworm are normally present in low numbers and feed primarily on Douglas-fir trees (Harris et al. 1985). Population outbreaks resulting in visible foliage damage are associated with density increases of 40% or more relative to endemic levels. Outbreaks of this intensity are the result of improved reproduction and survival rates, or spread from other infested locations (Campbell 1993).

Defoliation severely reduces the radial growth of trees by destroying photosynthetic tissue, thereby reducing the supply of carbohydrates needed for growth (Kramer and Kozlowski 1979). The ultimate effect of defoliation on growth is strongly influenced by the species of tree and insect, as well as by the intensity and timing of feeding, location in the crown, age and type of foliage destroyed, and physiological condition of the tree (Mason et al. 1997). The width of annual rings produced during infestation years is progressively reduced with each additional year of defoliation, in a cause-effect relationship that usually has a lag of 1 or more years (Alfaro and MacLauchlan 1992). After the infestation collapses, defoliated trees take several years to regain their full foliage; during this period radial-growth rates slowly recover. In addition, severe defoliation events that extend over a number of years often cause mortality of the upper crown due to a type of damage known as dieback or top kill. Trees that survive dieback resume height growth through lateral branches gaining apical dominance or by means of branches that originate from adventitious buds on the main stem (Alfaro and MacLauchlan 1992).

Two factors related to bud development have a marked effect on the rates of establishment and survival of western spruce budworm larvae: the degree of synchronization between bud swelling and larval emergence from overwintering, and the development time remaining for the insects after the buds have flushed (Cleary and Waring 1969). The degree of synchronization varies from year to year because bud flushing is dependent on root temperature as well as air temperature (Cleary and Waring 1969), whereas larvae respond only to air temperature (Shepherd 1992). However, the western spruce budworm overcomes the lack of perfect synchronization by maintaining flexibility in the dates of emergence from overwintering (Volney et al. 1983), thus bracketing the ideal stage for bud penetration. This behaviour helps to guarantee continuance of the species but can lead to large reductions of population density in years of poor synchrony. A similar effect has been found with other closely related tree species where bud flushing dates are important for the establishment of spruce budworm (*Choristoneura fumiferana* (Clemens)), primarily on *Picea* spp. and *Abies* spp., large aspen tortrix (*Choristoneura conflictana* (Walker)) largely on *Populus tremuloides* Michx., and oblique-banded leaf roller (*Choristoneura rosaceana* (Harris)) predominantly on members of the family Rosaceae.

Climatic variations, such as those that accompany wet and dry episodes, also increase or decrease the vulnerability of trees to insect attack (Ryerson et al. 2003). Although only limited research has been undertaken to examine the effect of climate on western spruce budworm infestations in the IDF zone of British Columbia (Thomson et al. 1984), Thomson (1979) has emphasized the importance of climate

in establishing synchrony between larval emergence and bud flush. Similarly, in northern New Mexico, Swetnam and Lynch (1993) noted a positive relationship between spring and early-summer precipitation levels and the occurrence of regional-scale outbreaks. More recently, Ryerson et al. (2003) reported that western spruce budworm outbreaks in the mixed conifer forests of south-central Colorado typically correspond to times of increased moisture.

In the IDF zone of British Columbia, coniferous trees respond to climate, insect attack, fire, and other disturbances with changes in the width of their annual growth rings (Campbell et al. 2005). Consequently, a disturbance record is retained in the tree rings that can be examined using standard dendroecological techniques (Fritts and Swetnam 1989) to determine the magnitude and frequency of these events (Wickman et al. 1994; Zhang et al. 1999). For example, the effects of *Choristoneura* spp. outbreaks on radial growth of trees can be inferred by comparing tree-ring chronologies from host and non-host species at neighbouring sites (Swetnam and Lynch 1993; Ryerson et al. 2003).

The purpose of this research was to establish a history of budworm outbreaks in representative IDF stands near Kamloops, British Columbia, and to document any relationships between historical western spruce budworm infestations and climatic variables. In this study, tree-ring chronologies from host and non-host trees were compared with historical forest insect and weather-station records to examine the relationship between climate and the onset and duration of western spruce budworm outbreaks (Swetnam et al. 1999; Ryerson et al. 2003). It was anticipated that these findings would provide an opportunity to present a perspective on the likely response of western spruce budworm to impending climate changes in the dry Douglas-fir forests of interior British Columbia.

Materials and methods

Study area

Field investigations focused on forest stands located near Kamloops (50°49'31"N, 120°28'20"W) in the summer of 2001. The IDF zone occurs in the rain shadow of the Coast Mountains throughout the southern and central interior of British Columbia. Annual total precipitation ranges from 295 to 750 mm and mean annual air temperature ranges from 1.6 to 9.5 °C (Meidinger and Pojar 1991). The study area is characterized by mixed stands of Douglas-fir and ponderosa pine at low to mid elevations (300–1250 m a.s.l.) and Douglas-fir and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) at high elevations (1130–1450 m a.s.l.) (Parish et al. 1996). Open grasslands are common in the drier regions, and pinegrass (*Calamagrostis rubescens* Buckl.) is a common understory species throughout the zone (Lloyd et al. 1990).

Twenty chronologies of Douglas-fir (host) trees and 11 chronologies of ponderosa pine (non-host) trees were selected from within a 325 km² area of documented historic defoliation. Douglas-fir trees with a diameter at breast height (DBH) >42 cm and exhibiting crown defoliation were selected. Ponderosa pine trees within or adjacent to defoliated stands were selected. Increment borers were used to extract

two cores per tree at DBH (1.3 m height) from a minimum of 20 trees per site.

Laboratory analysis

The cores were air-dried and polished with progressively finer sandpaper to enhance visibility of the annual-ring boundaries. A WinDENDRO™ (Version 6.1b) digital tree ring image processing and measuring system (Guay et al. 1992) and a Velmex-type stage were used to measure annual-ring increments to the nearest 0.01 mm. The measured tree-ring sequences were visually cross-dated by identifying key ring-width features (Stokes and Smiley 1968) and statistically cross-dated using the International Tree-Ring Data Bank software program COFECHA (Holmes 1994). In this instance, verification was based on 50-year dated segments with a 25-year lag, at a 99% critical-level correlation of 0.32 (Fritts 1976). Segments that did not cross-date were deleted or corrected until a significant correlation was obtained for all series, including each stand chronology.

A double-detrending procedure within the computer program ARSTAN (Holmes 1994) was used to produce standardized ring-width indices. Standardization of the tree-ring series is necessary to remove age-related trends in growth so that other factors causing growth variation can be evaluated separately (i.e., insects, fire, and climate). The ring-width series were standardized using a two-step process where a negative exponential and a cubic spline (50% frequency response, with 100-year minimum lengths and 67% rigidity, minimum rigidity 32 years) were applied to the series (Cook and Kairiukstis 1990). Douglas-fir ring-width indices were averaged into site chronologies using a biweight robust mean (Cook and Holmes 1986). Non-host chronologies were clustered into a single geographical grouping, to minimize site-specific nonclimate responses and enhance species-specific climate responses for comparison with those of the host species.

Ring-width measurements from stands known to have been defoliated by the western spruce budworm in the 20th century were examined both visually and statistically. The characteristic ring-width pattern of suppressed growth associated with western spruce budworm defoliation was identified based on the timing, duration, and magnitude of ring-width reductions in the stands. This characteristic signature was used to calibrate the software program OUTBREAK Version 6.00P, which automates the analysis of site-specific host tree-ring chronologies (Holmes and Swetnam 1996). OUTBREAK applies a set of user-defined criteria for identifying possible insect-outbreak periods and related growth reduction in each site chronology (Ryerson et al. 2003). Specifically, a minimum threshold was set whereby a minimum of 8 years of below-average growth and a reduction in growth below -1.28 standard deviation during at least 1 year was needed to identify an outbreak (Ryerson et al. 2003). Two periods of growth release prior to and after the maximum growth reduction were permitted, as this allowed for the possibility of a year with increased radial growth when larval populations may have temporally declined before release. These parameters were used to determine outbreak events prior to the 20th century (AD 1700–1900). To

differentiate between an outbreak and incipient events (or background noise), outbreak duration and growth reduction were summarized for periods at each stand for outbreaks with a growth reduction recorded for 35% or more trees.

The Forest Insect and Disease Survey (FIDS) of the Canadian Forestry Service monitored defoliator populations and the damage they caused between 1912 and 1994 at sites throughout British Columbia. In 1995, the British Columbia Ministry of Forests assumed responsibility for the annual monitoring of forest health and is currently collecting data for the province. FIDS records for the study area indicate that between 1954 and 1963 the western spruce budworm was present only in low numbers. In the interval from 1964 to 1982 no outbreaks were detected in the study area. Beginning in 1983 and continuing through 1992, populations of budworm increased to outbreak levels, with defoliation intensities ranging from light to severe. From 1994 through 2000, zero to low defoliation levels were detected by means of aerial or ground surveys (Erickson 1987; British Columbia Ministry of Forests 2001).

Climate and the seasonal timing of infestations are also factors that need to be considered in dendroecological reconstructions of insect outbreaks (Fritts 1991). Similarity of climate response in host and non-host species is necessary for identifying insect outbreaks in host trees (Ryerson et al. 2003). Research previously conducted on Douglas-fir and ponderosa pine trees growing in comparable sites and regions established that the two species have a common radial-growth response to climate (Fritts 1974; Swetnam et al. 1985). To test for similarity between the two species in our study area, response functions were developed.

Response-function analysis was used to define the radial-growth response of regional Douglas-fir and ponderosa pine tree-ring chronologies to precipitation and air temperature (Fritts et al. 1991) recorded at Kamloops, British Columbia, from 1895 to 1998 (http://www.cccma.bc.ec.gc.ca/hccd/data/access_data.html). The software program PRECON 32 (Version 5.17b) (Fritts et al. 1991) was used to verify that ponderosa pine was a suitable non-host, a control for climate in our study area.

To control for climatic influences, the host (Douglas-fir) and non-host (ponderosa pine) chronologies were compared graphically and statistically to construct a western spruce budworm signal (Swetnam et al. 1995). The “corrected” tree-ring indices were calculated with the following equation:

$$[1] \quad \text{Corrected Index} = I_{ht} - \frac{SD_h}{SD_n} (I_{nt} - \bar{I}_n)$$

where I_{ht} is the host tree-ring index at year t , SD_h is the standard deviation of the individual host tree series for the period common to the two series, SD_n is the standard deviation of the non-host composite chronology for the period common to the two series, I_{nt} is the non-host tree-ring index at year t , and $\bar{I}_n$ is the mean of the non-host tree-ring index for the period common to the two series.

“Corrected” tree-ring indices serve as records of radial growth in the host tree after reduction or elimination of climate signals as indicated by the non-host trees. The year of maximum growth reduction for each outbreak was defined

Table 1. Location and characteristics of the site chronologies from Douglas-fir (DF) and ponderosa pine (PP) sampled near Kamloops, British Columbia.

Location	Site	Species	Latitude N	Longitude W	Elevation (m a.s.l.)	Aspect
Mud Lake	AA	DF	50°48'	120°25'	983	Variable
	AA	PP	50°48'	120°25'	983	Variable
	AB	DF	50°48'	120°27'	985	S
	AB	PP	50°48'	120°27'	985	S
	AC	DF	50°48'	120°27'	910	SE
	AC	PP	50°48'	120°27'	910	SE
	AD	DF	50°49'	120°27'	1113	SE
	AD	PP	50°49'	120°27'	1113	SE
	AE	DF	50°49'	120°27'	1103	SE
	AG	DF	50°49'	120°28'	1078	SE
	AI	DF	50°49'	120°28'	1004	NE
	AJ	DF	50°49'	120°28'	1090	S
Hanging Valley	AK	DF	50°46'	120°29'	970	NW
	AL	DF	50°46'	120°29'	998	NW
	AL	PP	50°46'	120°29'	998	NW
	AM	DF	50°46'	120°28'	980	Variable
	AN	DF	50°46'	120°28'	1010	Variable
	AN	PP	50°46'	120°28'	1010	Variable
	AR	PP	50°48'	120°28'	850	SE
	AT	PP	50°47'	120°28'	800	N
Opax Mountain	AF	DF	50°49'	120°28'	1239	SE
	AO	DF	50°49'	120°30'	1239	S
	AP	DF	50°49'	120°29'	1275	Variable
	AQ	DF	50°49'	120°29'	1307	Variable
	AU	DF	50°49'	120°29'	1362	N
	AV	DF	50°49'	120°28'	1380	N
Lac du Bois road	AH	DF	50°50'	120°31'	839	NE
	AH	PP	50°50'	120°31'	839	NE
Tranquille Valley	Tranquille ^a	PP	50°46'	120°39'	850	S
	Fritts ^a	PP	50°46'	120°36'	700	NW

^aChronology provided by E. Watson (Watson and Luckman 2002).

as the mean series index value minus the smallest index value during an outbreak. Periodic growth reduction for each outbreak was defined as the mean series index value minus the mean index value during outbreaks. In both cases the "mean series index value" is 1.0 (denoting potential growth) in standardized ratio indices. Values less than 1.0 in the tree-ring indices indicate reduced growth with respect to potential growth; values greater than 1.0 indicate increased growth. OUTBREAK calculated the mean radial growth trends for all trees in each stand and listed the timing, level of growth reduction, and duration of the outbreaks detected for each tree and for the entire stand.

The timing of the infestation periods identified by OUTBREAK was verified by scrutinizing the dated tree-ring specimens and comparing them with confirmed historical defoliation episodes from FIDS and British Columbia Ministry of Forests aerial survey records from the 20th century (Erickson 1987; British Columbia Ministry of Forests 2001). The duration and extent of outbreak events were evaluated by examining the composite percentage of trees for which outbreaks were recorded.

A regional time series of outbreaks was computed by summing the numbers of trees for which an outbreak was recorded during each year for the entire record across all

stands. The number of trees included in the record decreased with increasing time before the present, so the series were standardized by computing the percentage of trees for which an outbreak was recorded in each year.

Coincidences of western spruce budworm outbreaks and wet/dry periods in the precipitation record were analyzed using stepwise regression analysis. The regional outbreak series were compared with precipitation and temperature data divided into mean temperature and total monthly precipitation variables for winter (November–February), spring (March–June), and summer (July–October).

We used singular spectrum analysis (SSA) to assess whether there were cyclical patterns of western spruce budworm populations in the tree-ring record in forests in the IDF zone. SSA is a nonparametric method of analyzing time series that utilizes principal component analysis to provide a more in-depth assessment of the time-series properties of the data. SSA permits the user to evaluate cyclical behaviour in a single time series by extracting pairs of "reconstructed components" or "sine-cosine waves" that represent the dominant cyclical periods of the data. Because the "waveforms" retain the temporal characteristics of cyclical behaviour, it is possible to detect changes in amplitude and phasing of dominant cycles (Speer et al. 2001).

Table 2. Length, interserial correlation, and mean sensitivity of master chronologies for Douglas-fir at 19 sites near Kamloops, British Columbia, used to study patterns of western spruce budworm outbreak.

Site ^a	Chronology period (AD)	No. of years	Interserial correlation	No. of trees cored	Mean sensitivity	Autocorrelation ^b	Correlation coefficient ^c
AA	1828–2001	173	0.61	9	0.29	0.74	0.57
AB	1903–2001	98	0.65	14	0.32	0.62	0.49
AC	1898–2001	103	0.63	16	0.30	0.58	0.48
AD	1722–2001	279	0.51	14	0.29	0.73	0.32
AE	1764–2000	237	0.61	13	0.27	0.74	0.63
AF	1855–2001	146	0.62	16	0.24	0.74	0.57
AG	1829–2001	172	0.64	15	0.25	0.73	0.55
AH	1815–2001	186	0.68	16	0.27	0.84	0.67
AI	1809–2001	192	0.60	16	0.21	0.80	0.37
AJ	1733–2000	267	0.62	16	0.27	0.72	0.66
AK	1704–2001	297	0.47	13	0.31	0.70	0.45
AL	1600–2001	401	0.53	14	0.29	0.70	0.72
AM	1651–2001	350	0.59	16	0.32	0.74	0.68
AN	1623–2001	378	0.72	14	0.31	0.69	0.37
AO	1672–2000	328	0.55	16	0.25	0.78	0.42
AP	1631–2001	370	0.54	16	0.28	0.78	0.44
AQ	1648–2001	353	0.49	17	0.25	0.79	0.56
AU	1727–2001	274	0.66	17	0.25	0.73	0.61
AV	1653–2000	347	0.61	16	0.22	0.76	0.65
Mean			0.60	16	0.27	0.73	0.54
Master chronology							
Pine ^d	1523–2001	478	0.63	65	0.32	0.72	
Douglas-fir	1600–2000	400	0.56	264	0.27	0.74	

^aFor locations of sites see Table 1.^bGrowth in any given year as it relates to growth in previous years.^cStrength of the relationship between the regional ponderosa pine chronology and each Douglas-fir site chronology.^dPortion of a pine chronology provided by E. Watson (Watson and Luckman 2002).

Results

Dendrochronological findings

A total of 19 Douglas-fir (284 trees, 568 cores) chronologies and 11 ponderosa pine chronologies (65 trees, 130 cores) were developed from 24 stands (Table 1). Eight of the Douglas-fir chronologies came from the Mud Lake area, four were from Hanging Valley, six from Opax Mountain, and one from a site along the Lac du Bois road. The 11 ponderosa pine chronologies were combined to create a regional chronology for the study area. The mean interserial correlation, describing the average pairwise correlations within each of the 19 detrended Douglas-fir chronologies, ranged from 0.47 to 0.72 (Table 2). These findings indicate that the trees responded similarly to common environmental influences over the period of record. Mean sensitivity describes the interannual variation in ring width as a proportion of the local mean ring width. In the case of Douglas-fir, mean sensitivity ranged from 0.21 to 0.32, indicating low to moderate interannual variation in the tree-ring series (Table 2). Serial autocorrelation, which indicates the degree of relationship between successive values within each chronology time series, ranged from 0.58 to 0.84. All 19 Douglas-fir stand chronologies were significantly correlated ($p < 0.05$) with the regional ponderosa pine chronology over the period from AD 1600 to 2000. Correlation coefficients ranged from 0.32 to 0.72 (Table 2). These findings suggest that the Douglas-fir stand chronologies within the IDF zone contain a common

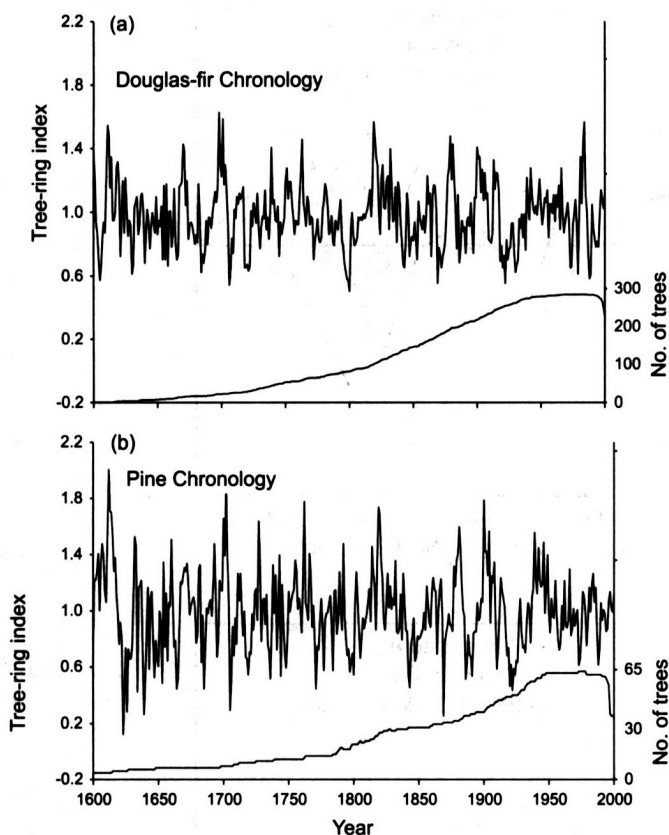
radial-growth signal, a finding similar to that reported by Watson and Luckman (2001, 2002), who attributed similar radial-growth behaviour to regional climatic conditions. Cores contributing to the Douglas-fir regional chronology span the interval from AD 1600 to 2000 (mean interserial correlation 0.56, mean sensitivity 0.27, mean autocorrelation 0.74; Table 2, Fig. 1).

Douglas-fir and ponderosa pine trees found growing in comparable sites proved to have similar growth responses to climate. The response functions for Douglas-fir trees indicate that 34.6% of the interannual variation in radial growth can be attributed to climate (Fig. 2). Radial growth of Douglas-fir trees was significantly and positively correlated with both precipitation in August of the growth year and precipitation in November and January in the previous winter. Significant negative correlations with June air temperatures indicate that warmer than average conditions limit radial growth. The response functions calculated for ponderosa pine indicate that 32.5% of the interannual variation in radial growth can be attributed to climate (Fig. 2). Ring growth of ponderosa pine was significantly and positively correlated with November and December precipitation in the previous year and negatively correlated with air temperature in August and September of the previous year and June of the growth year.

Frequency of outbreaks

The most recent defoliation event identified by OUT-

Fig. 1. Master chronologies of Douglas-fir (a) and ponderosa pine (b) near Kamloops, British Columbia, from AD 1600 to 2000, and numbers of trees contributing to each year of the chronology.



BREAK is also documented in the historical records. Between 1985 and 1995, western spruce budworm outbreaks were confirmed at 60% of our stands and all appear in the tree rings within 1–2 years of their recorded occurrence (Koot and Hodge 1995) (Fig. 3). This lagged radial-growth response is attributed to previously stored photosynthates that permit cambial development to continue even after a tree is defoliated (Alfaro et al. 1982). While the lag in radial-growth reduction limits the temporal precision of our reconstructions of outbreaks within a given stand, it is accepted that regional western spruce budworm events do not start in a single year throughout the budworm range, and that a spatial lag may occur (Swetnam and Lynch 1993). The outbreak reconstruction also indicates that a defoliation event occurred in the mid-1920s at 82% of the sites (Fig. 3); this event is not documented in the FIDS records (AD 1912–2000). This may be a result of parsimonious sampling during this period.

Reconstruction of western spruce budworm outbreaks at the stand level revealed tree-ring evidence for outbreak events in this area as early as AD 1600 (Fig. 4). While our confidence in reconstructing regional western spruce budworm outbreaks prior to the early 1700s declines as the number of chronologies in the sample decreases, we have distinguished eight outbreak events, at the stand level, over the last 300 years of the tree-ring record. These outbreaks started in the ~1700s, early 1720s, early 1750s, mid-1780s, ~1810, ~1890s, mid-1920s, and 1985 (Fig. 4). Outbreaks

within the region occurred in the early 1720s, early ~1810s, and ~1890s in 50%, 47%, and 63% of the stands, respectively (Fig. 4).

Periodicity of outbreaks

Three significant cycles with dominant wavelengths were identified using SSA: a ~30-year cycle explaining 24% of the variance; a ~43-year cycle explaining 22% of the variance; and a ~70-year cycle explaining 15% of the variance. Overall, the three cycles explained 61% of the variance in the outbreak time series. The temporal harmonics of the three cycles suggest that significant outbreak events are coincident with intervals when the maxima of all three coincide (Fig. 5). This synchronicity is most notable in the 1760s (peak of the early-1750s outbreak), the 1830s (peak of the ~1810 outbreak), 1910s (peak of the ~1890s outbreak), 1940s (peak of the mid-1920s outbreak), and 1990s (peak of the 1985 outbreak). Interestingly, while the harmonics of the ~30- and ~70-year cycles remained relatively stable through the period of record, the ~43-year cycle was quiescent in amplitude until the late 19th century. The distinctive amplitude expansion of the ~70-year cycle in the 20th century was in phase with both the ~30- and ~43-year cycles, and is coincident with the peak of the large outbreaks in ~1910, ~1946, and ~1996 (Fig. 5).

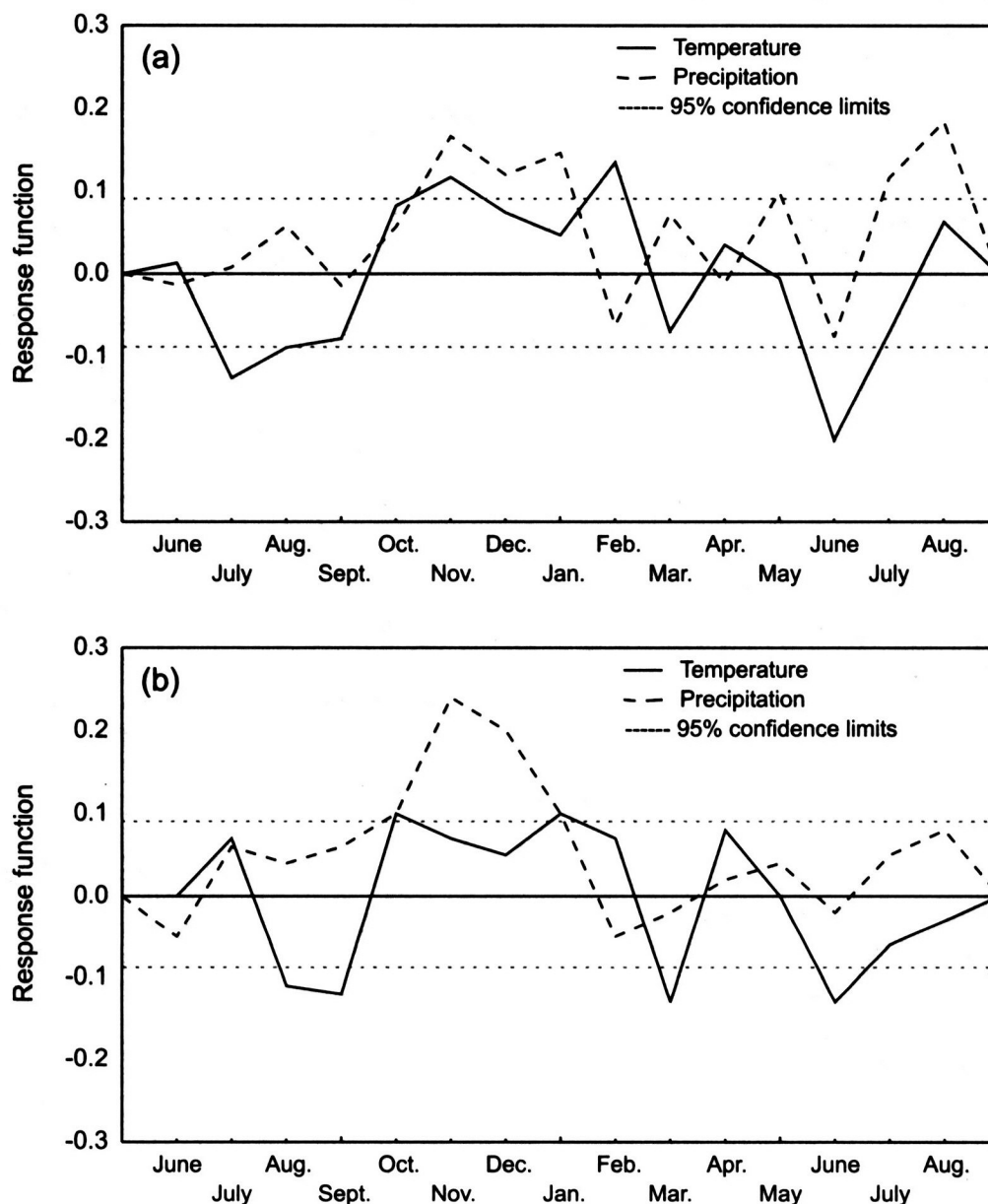
Relationship between budworm outbreaks and climate

Analyses of the Kamloops climate record revealed a weak negative correlation between total seasonal precipitation and mean annual air temperature: lower precipitation levels corresponded to higher air temperatures. Between 1895 and 1998, total annual precipitation was 302 ± 60 mm/year (mean $\pm$ SD) and annual air temperature was 8.4 ± 0.93 °C. During the two outbreak periods recorded in the 20th century (mid-1920s and mid-1980s), total annual precipitation dropped to below 200 mm/year and mean annual air temperatures exceeded the long-term average by 0.6 °C (1930s) and 2.1 °C (mid-1980s). In this instance, a comparison of the outbreak chronology (not shown) and climate showed a strong positive relationship between winter (November–February) precipitation and outbreak occurrence ($r^2 = 0.40$) (Fig. 6). The outbreak in the late 19th century (~ mid-1890s) also occurred during a period of reduced winter precipitation but prior to the official collection of insect records (Fig. 6).

Discussion

Tree-ring data from this study have confirmed eight western spruce budworm outbreaks at forest sites near Kamloops in central British Columbia over the last 300 years. Of these, the two outbreaks that occurred in the 20th century are documented in insect survey records. The western spruce budworm outbreaks in the mid-1920s and mid-1980s occurred during periods of low winter precipitation as deduced from the ponderosa pine chronology and instrumental records. This is supported by the findings of Thomson et al. (1984), who noted a negative relationship between precipitation levels and severe western spruce budworm infestations. Campbell (1989) suggested that western spruce budworm larvae that fed on foliage from early spring were 20% heavier and had 25% higher fecundity than larvae that fed

Fig. 2. Response functions for Douglas-fir (a) and ponderosa pine (b) tree-ring chronologies using weather data from Kamloops. Monthly climate interval variables for the period AD 1895–1998 are used to explain the variance in tree-rings. Peaks above and below the 95% confidence limits indicate the months in which growth was most influenced by either temperature or precipitation.



on foliage from late spring. This observation suggests that the annual variations in spring climate affect the nutrient quality of foliage.

Our comparisons of climate with budworm outbreaks show a positive relationship between low winter precipitation levels and the start of the growing season and the occurrence of outbreaks. While site-specific patterns were distinctive, a high degree of synchrony between the study sites was apparent, particularly prior to the 1800s and during the 1900s. Coincident outbreaks during the early, middle, and late 1700s also occurred in the three regions. The patterns exhibited in our study area are not unique. Both Ryerson et al. (2003) and Swetnam and Lynch (1993) reported a persistent regional cadence of western spruce budworm outbreaks within their study areas in New Mexico and Colorado, respectively.

This synchronization of outbreaks requires that insect populations be exposed to a common endogenous factor able to harmonize their population oscillations. Jardon et al. (2003) suggests that a common environmental cue called the Moran effect acts on minor fluctuations in insect populations and helps to synchronize those that are oscillating at different densities over the landscape. As Watson and Luckman (2004) have demonstrated, the temporal and spatial synchrony of annual precipitation and mean air temperature are both significant and measurable within the IDF zone of British Columbia. These climate variables may act as environmental cues capable of producing a synchronizing effect on western spruce budworm populations within this area (Koenig 2002).

In contrast, stand-specific outbreaks during the 1800s were generally not synchronous. This lack of synchrony oc-

Fig. 3. Percentages of Douglas-fir trees with reduced growth relative to ponderosa pine. A minimum of $\geq 35\%$ of trees in a given year must exhibit reduced growth to be classified as having sustained a western spruce budworm outbreak. Eight outbreaks were identified in the study area.

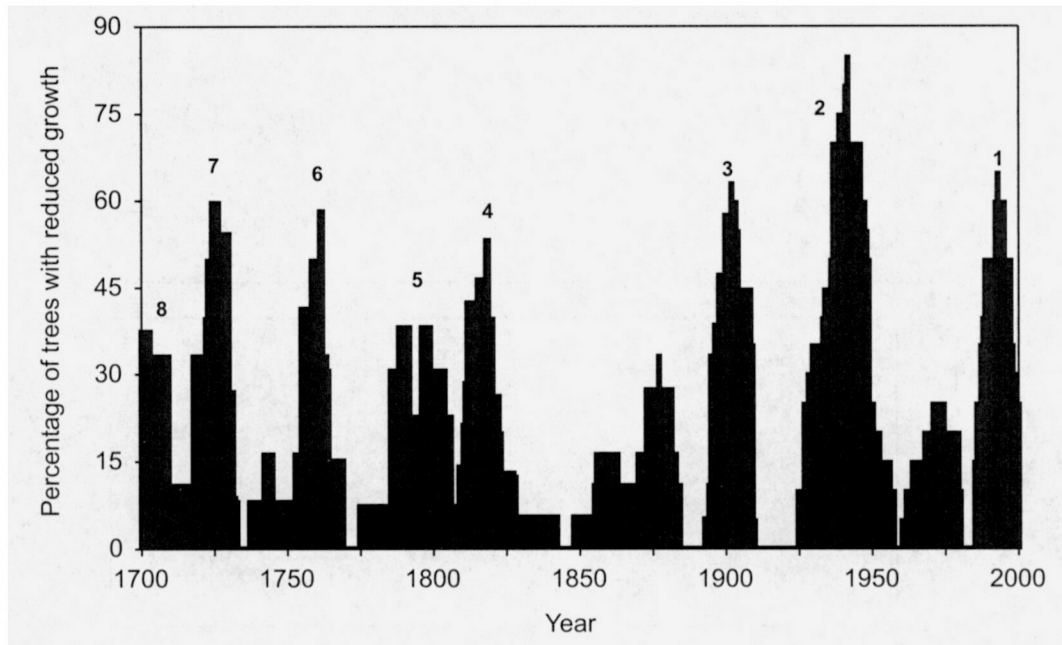
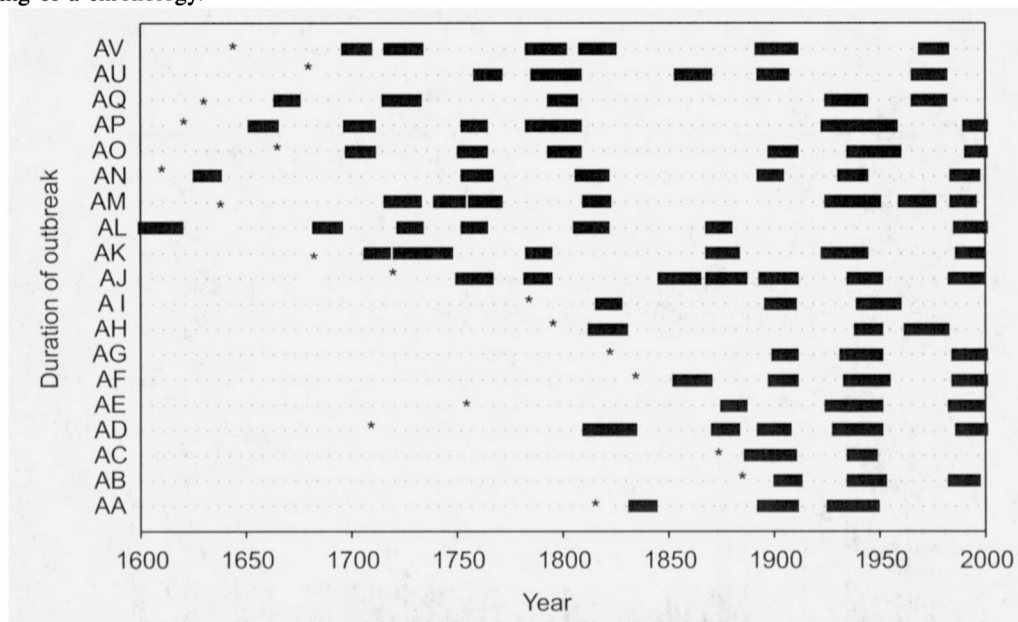


Fig. 4. Periods of reduced growth of Douglas-fir relative to ponderosa pine, which indicate the possible timing and duration of western spruce budworm outbreaks in interior Douglas-fir forests near Kamloops, British Columbia, from AD 1600 to 2000. The duration of infestations (solid bars) was inferred from chronologies for each Douglas-fir stand. For locations of sites see Table 1. An asterisk indicates the beginning of a chronology.



curred during a time (1840–1923) when alternating regimes of relatively warm and cool sea-surface temperatures in the North Pacific Ocean, driven by the Pacific Decadal Oscillation, affected climates throughout the Pacific Northwest (Gedalof and Smith 2001).

Given that climate directly and indirectly influences forest dynamics, it may be that extrinsic factors related to large-scale climate play a critical role in synchronizing the dynamics of western spruce budworm populations. Positive

correlations of growth of both Douglas-fir and ponderosa pine with precipitation in winter (November–February), prior to the growing season, suggest that nongrowing-season precipitation (i.e., snowpack) is more important than growing-season precipitation. Low precipitation levels during the winter months and normal spring air temperatures, which characterize an early spring season, act as cues for budworm to emerge (Perry and Pitman 1996). Beckwith and Burnell (1982) found that in north-central Washington State,

Fig. 5. Singular spectrum analysis (59% of variance explained) of western spruce budworm time series illustrating the periodicity of outbreaks each year since the 1700s.

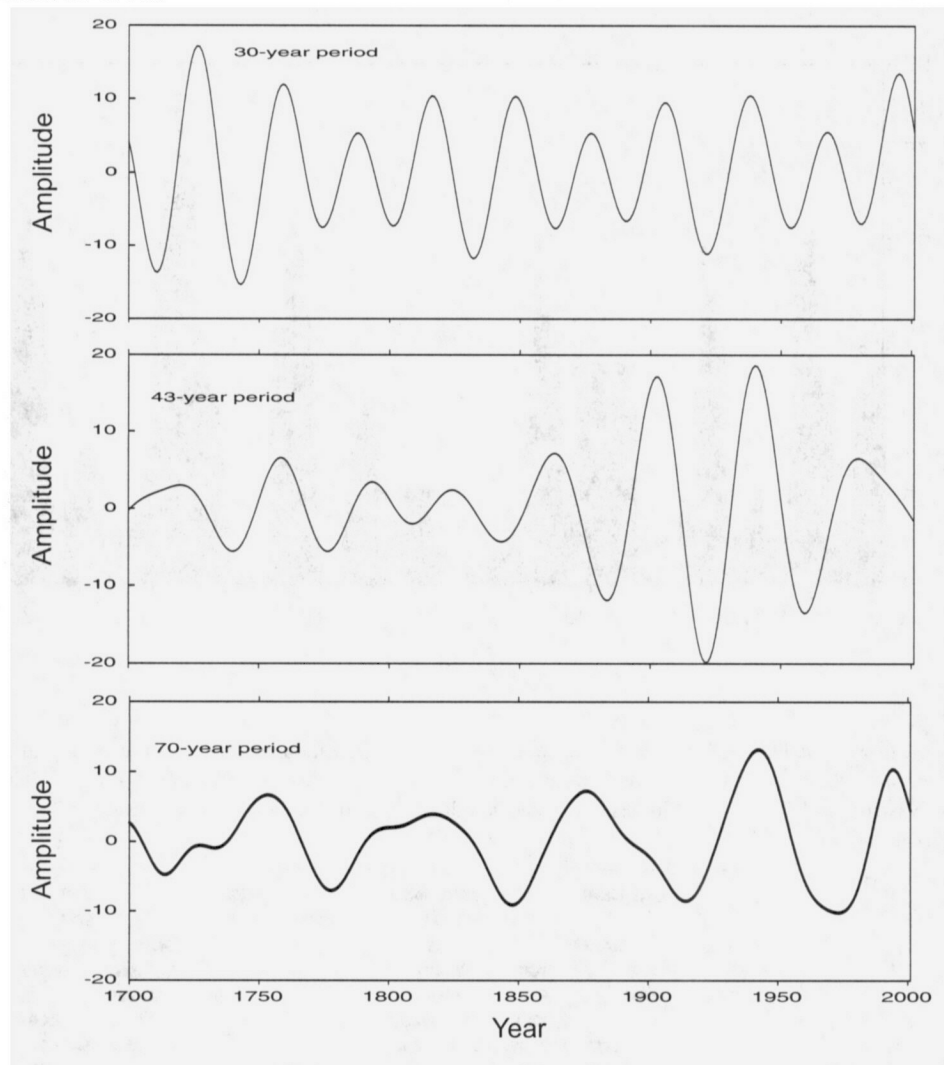
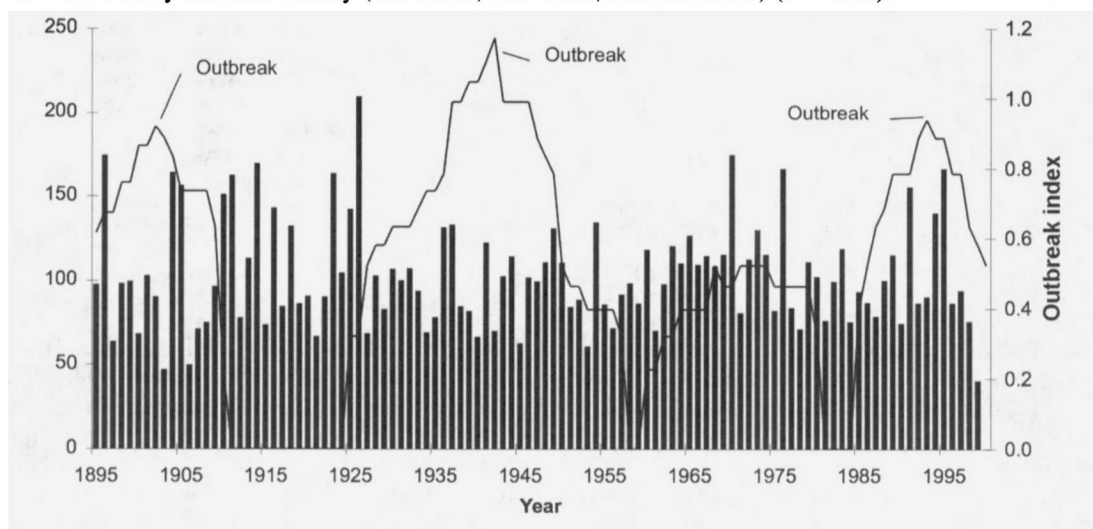


Fig. 6. Comparison of winter (November–February) precipitation (AD 1895–2000) with western spruce budworm outbreak periods recorded in the late 19th century and 20th century (mid-1890s, mid-1920s, and mid-1980s) ($r^2 = 0.40$).



climatic conditions in spring were such that budworm emerged before buds began swelling. Under these circumstances, western spruce budworm were forced to feed on older foliage or seek a new host, either of which results in high budworm mortality.

The positive effect of spring precipitation on radial growth of Douglas-fir suggests that water availability during the growing season is one factor limiting radial growth of Douglas-fir, an observation consistent with information from other regions (Zhang et al. 1999). The positive effect of high temperatures and precipitation levels in late fall on ring-width growth of Douglas-fir suggests that warm, moist days in late fall favour active photosynthesis and continuous food storage, leading to large ring widths in the following year (Fritts 1976; Waring and Franklin 1979). In contrast, researchers in Colorado and New Mexico found that outbreaks show a positive relationship between spring and early-summer precipitation (Swetnam and Lynch 1993; Ryerson et al. 2003).

Western spruce budworm population outbreaks at ~30- to ~43- and ~70-year intervals were identified in the IDF zone tree-ring record. Proxy climate reconstructions and climate data from Kamloops show that strong but temporally variable western spruce budworm cycles were in phase with and perhaps entrained by weak precipitation cycles as shown by the three outbreak periods recorded in the 20th century. This synchrony was most notable when total annual precipitation dropped below 200 mm/year and mean annual air temperatures exceeded long-term values by 0.6 °C (1930s) and 2.1 °C (mid-1980s). The waveforms extracted by SSA disaggregate the dominant cycles and indicate that during certain decades and centuries the amplitudes of these cycles were in unusually high or low phase with each other. The temporal synchrony in outbreak events reported here is similar to that documented for other *Choristoneura* species. Ryerson et al.'s (2003) New Mexico study indicates periodicities of ~25, ~37, and ~83 years, whereas Swetnam and Lynch's (1993) Colorado study showed ~20- and 33-year periodicities. Jardon et al. (2003) reports that different types of outbreak dynamics can be found within the same insect species and that combined periodicities are the result of migration effect, local population dynamics, and common regional environmental factors.

Conclusion

This research demonstrates that western spruce budworm outbreaks in this portion of the Kamloops Forest Region have occurred periodically over the last 300 years. This long-term perspective was provided by examining insect-derived radial-growth signatures within the tree rings of long-lived stands of Douglas-fir that sustained approximately eight regional outbreaks over a period of three centuries. This tree-ring record indicates that some overstory trees can coexist with budworm for long periods of time. This relationship is similar to that found by previous researchers (Swetnam and Lynch 1993; Swetnam et al. 1995; Ryerson et al. 2003) and appears to occur even when defoliation caused by western spruce budworm populations does not reach the same level in all trees (Myers 1993; Bjørnstad 2000).

Analysis of climate and budworm dynamics using SSA revealed significant outbreak events with periodicities of both

~30 and ~43 years. It is suspected that forest characteristics precondition western spruce budworm populations to succeed and that the regional climate has a synchronizing influence (Royama 1984; Williams and Liebhold 1995, 2000; Myers 1998).

This study has shown that western spruce budworm outbreaks coincide with early spring seasons characterized by low precipitation levels during the winter months and normal spring air temperatures. This observation suggests that these climatic conditions enhance budworm emergence and reduce Douglas-fir trees' capacity for defence against foraging activity. Research involving simultaneous observations of insect numbers, defoliation levels, and tree-ring growth parameters is required to test the fidelity of the host – non-host correction approach in reconstructing past outbreaks and to examine the role played by climate variation in western spruce budworm dynamics.

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References

- Alfaro, R.I., and MacLauchlan, L. E. 1992. A method to calculate the losses caused by western spruce budworm in uneven-aged Douglas fir forests of British Columbia. *For. Ecol. Manage.* **55**: 295–313.
- Alfaro, R.I., Van Sickle, G.A., Thomson, A.J., and Wegwitz, E. 1982. Tree mortality and radial growth losses caused by western spruce budworm in a Douglas-fir stand in British Columbia. *Can. J. For. Res.* **12**: 780–787.
- Beckwith, R.C., and Burnell, D.G. 1982. Spring larval dispersal of the western spruce budworm in north-central Washington. *Environ. Entomol.* **11**: 828–832.
- Bjørnstad, O.N. 2000. Cycles and synchrony: two historical experiments and one experience. *J. Anim. Ecol.* **69**: 869–873.
- British Columbia Ministry of Forests. 2001. Forest Health Aerial Overview Survey. Forest Practices Branch, British Columbia Ministry of Forests, Victoria, B.C.
- Brubaker, L.B., and Greene, S.K. 1979. Differential effects of Douglas-fir tussock moth and western spruce budworm defoliation on radial growth of grand fir and Douglas-fir. *Can. J. For. Res.* **9**: 95–105.
- Campbell, I.M. 1989. Does climate affect host-plant quality? Annual variation in the quality of balsam fir as food for spruce budworm. *Oecologia*, **81**: 341–344.
- Campbell, R.C., Smith, D.J., and Arseneault, A. 2005. Dendroentomological and forest management implications in the Interior Douglas-fir zone of British Columbia, Canada. *Dendrochronologia*, **22**: 135–140.

- Campbell, R.W. 1993. Population dynamics of the major North American needle-eating budworms. US For. Serv. Res. Pap. PNW-RP-463.
- Cleary, B.D., and Waring, R.H. 1969. Temperature: collection of data and its analysis for the interpretation of plant growth and distribution. *Can. J. Bot.* **47**: 167–173.
- Columbia Mountains Institute of Applied Ecology. 2005. Implications of climate change in British Columbia's Southern Interior Forests, April 26–27, 2005. Columbia Mountains Institute of Applied Ecology, Revelstoke, B.C.
- Cook, E.R., and Holmes, R.L. 1986. User's manual for program ARSTAN. In *Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin*. Edited by R.L. Holmes, R.K. Adams, and H.C. Fritts. Chronology Ser. VI, University of Arizona, Tucson, Ariz. pp. 50–56.
- Cook, E.R., and Kairiukstis, L. (Editors). 1990. *Methods of dendrochronology: applications in environmental sciences*. Kluwer, Dordrecht, Netherlands.
- Erickson, R.D. 1987. Maps of major forest insect infestations: Kamloops Forest Region 1912–1986. *Can. For. Serv. Pac. For. Cent. FIDS Rep.* 87–8.
- Fritts, H.C. 1974. Relationships of ring-widths in arid-site conifers to variations in monthly temperature and precipitation. *Ecol. Monogr.* **44**: 411–440.
- Fritts, H.C. 1976. *Tree rings and climate*. Academic Press, London.
- Fritts, H.C. 1991. *Reconstructing large-scale climatic patterns from tree-ring data*. University of Arizona Press, Tucson, Ariz.
- Fritts, H.C., and Swetnam, T.W. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Adv. Ecol. Res.* **19**: 111–188.
- Fritts, H.C., Vaganov, E.A., Sviderskaya, I.V., and Shashkin, A.V. 1991. Climatic variation and tree-ring structure in conifers: empirical and mechanistic models of tree-ring widths, number of cells, cell-size, cell-wall thickness and wood density. *Clim. Res.* **1**: 97–116.
- Gedalof, Z., and Smith, D.J. 2001. Interdecadal climate variability and regime-scale shifts in Pacific North America. *Geophys. Res. Lett.* **28**: 1515–1518.
- Guay, R., Gagnon, R., and Morin, H. 1992. A new automatic and interactive tree ring measurement system based on a line scan camera. *For. Chron.* **68**: 138–141.
- Harris, J.W.E., Alfaro, R.I., Dawson, A.F., and Brown, R.G. 1985. The western spruce budworm in British Columbia 1909–1983. *Can. For. Serv. Pac. For. Cent. Inf. Rep.* BC-X-257.
- Holmes, R.L., and Swetnam, T.W. 1996. Program OUTBREAK user's manual, Dendrochronology Program Library. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Ariz.
- Holmes, R.W. 1994. Dendrochronology Program Library user's manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Ariz.
- Jardon, Y., Morin, H., and Dutilleul, P. 2003. Périodicité et synchronisme des épidémies de la tordeuse des bourgeons de l'épinette au Québec. *Can. J. For. Res.* **33**: 1947–1961.
- Koenig, W. 2002. Global patterns of environmental synchrony and the Moran effect. *Ecography*, **25**: 283–288.
- Koot, P., and Hodge, J. 1995. History of population fluctuations and infestation of important forest insects in the Kamloops Forest Region 1912–1991. *Pac. For. Cent. For. Can. Rep.* 92–11.
- Kramer, P.J., and Kozlowski, T.T. 1979. *Physiology of trees*. Academic Press, New York.
- Lloyd, D., Angrove, K., Hope, G., and Thompson, C. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. B.C. Minist. For. Land Manage. Handb. 23. Parts 1 and 2.
- Mason, R.R., Wickman, B.E., and Paul, H.G. 1997. Radial growth response of Douglas-fir and grand fir to larval densities of the Douglas-fir tussock moth and the western spruce budworm. *For. Sci.* **43**: 194–205.
- Meidinger, D., and Pojar, J. 1991. *Ecosystems of British Columbia*. British Columbia Ministry of Forests, Victoria, B.C.
- Myers, J.H. 1993. Population outbreaks in forest Lepidoptera. *Am. Sci.* **81**: 240–251.
- Myers, J.H. 1998. Synchrony of outbreaks of forest Lepidoptera: a possible example of the Moran effect. *Ecology*, **79**: 1111–1117.
- Parent, S., Moran, H., and Messier, C. 2001. Balsam fir (*Abies balsamea*) establishment dynamics during a spruce budworm (*Choristoneura fumiferana*) outbreak: an evaluation of the impact of aging techniques. *Can. J. For. Res.* **31**: 373–376.
- Parish, R., Coupe, R., and Lloyd, D. 1996. *Plants of Southern Interior British Columbia*. Lone Pine Press, Edmonton, Alta.
- Perry, D. A., and Pitman, G.B. 1996. Genetic and environmental influences in host resistance to herbivory: Douglas-fir and the western spruce budworm. *Z. Angew. Entomol.* **96**: 217–228.
- Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecol. Monogr.* **54**: 429–462.
- Ryerson, D.E., Swetnam, T.W., and Lynch, A.M. 2003. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, U.S.A. *Can. J. For. Res.* **33**: 1010–1028.
- Shepherd, R.F. 1992. Relationships between attack rates and survival of western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae) and bud development of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. *Can. Entomol.* **124**: 347–358.
- Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A. 2001. Changes in Pandora moth outbreak dynamics during the past 622 years. *Ecology*, **82**: 679–697.
- Stokes, M.A., and Smiley, T.L. 1968. *An introduction to tree ring dating*. University of Chicago Press, Chicago, Ill.
- Swetnam, T.W., and Lynch, A.M. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecol. Monogr.* **63**: 399–424.
- Swetnam, T.W., Thompson, M.A., and Sutherland, E.K. 1985. Using dendrochronology to measure radial growth of defoliated trees. *US Dep. Agric. Agric. Handb.* 639.
- Swetnam, T.W., Wickman B.E., Paul, H.G., and Baisan, C.H. 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the northern Blue Mountains, Oregon, since A.D. 1700. *US For. Serv. Res. Pap.* PNW-484.
- Swetnam, T.W., Allen, C.D., and Betancourt, J.L. 1999. Applied historical ecology: using the past to manage the future. *Ecol. Appl.* **9**: 1189–1206.
- Thomson, A.J. 1979. Evaluation of key biological relationships of the western spruce budworm and its host trees. *Can. For. Serv. Pac. For. Cent. Inf. Rep.* BC-X-186.
- Thomson, A.J., Shepherd, R.F., Harris, J.W.E., and Silversides, R.H. 1984. Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in British Columbia. *Can. Entomol.* **116**: 375–381.
- Volney, W.J.A., Waters, W.E., Akers, R.P., and Leibhold, A.M. 1983. Variation in spring emergence patterns among western *Choristoneura* spp. (Lepidoptera: Tortricidae) populations in southern Oregon. *Can. Entomol.* **115**: 199–209.
- Waring, R.H., and Franklin, J.F. 1979. Evergreen coniferous forests of the Pacific Northwest. *Science (Washington, D.C.)*, **204**: 1380–1386.

- Watson, E., and Luckman, B.H. 2001. The development of a moisture-stressed tree-ring chronology network for the southern Canadian Cordillera. *Tree-Ring Res.* **57**: 149–168.
- Watson, E., and Luckman, B.H. 2002. The dendroclimatic signal in Douglas-fir and ponderosa pine tree-ring chronologies from the southern Canadian Cordillera. *Can. J. For. Res.* **32**: 1858–1874.
- Watson, E., and Luckman, B.H. 2004. Tree-ring based reconstructions of precipitation for the southern Canadian Cordillera. *Clim. Change*, **65**: 209–241.
- Wickman, B.E., Mason, R.R., and Swetnam, T.W. 1994. Searching for long-term patterns of forest insect outbreaks. *In* *Individuals, populations, and patterns in ecology*. Edited by S.R. Leather, K.F.A. Walters, N.J. Mills, and A.D. Watt. Intercept, Andover, UK. pp. 251–261.
- Williams, D.W., and Liebhold, A.M. 1995. Detection of delayed density dependence: effects of autocorrelation in an exogenous factor. *Ecology*, **76**: 1005–1008.
- Williams, D. W., and Liebhold, A. M. 2000. Spatial synchrony of spruce budworm outbreaks in eastern North America. *Ecology*, **81**: 2753–2766.
- Zhang, Q., Alfaro, R.I., and Hebda, R.J. 1999. Dendroecological studies of tree growth, climate and spruce beetle outbreaks in central British Columbia, Canada. *For. Ecol. Manage.* **121**: 215–225.