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

by

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Abstract

Western spruce budworm (*Choristoneura occidentalis* (Freeman)) is a native defoliator of the Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco) forests of British Columbia, Canada. This thesis used dendrochronology and the software program OUTBREAK to reconstruct a defoliation history of Douglas-fir for nineteen forest sites near Kamloops in central British Columbia. By comparing the radial growth response of non-host ponderosa pine trees to Douglas-fir trees growing in nearby but separate stands, seven western spruce budworm outbreaks were distinguished over the past 300 years. Although there is considerable variation in the timing and duration of these western spruce budworm events at the stand level, synchronous outbreaks have occurred at approximately 43-year intervals. Climate variation appears to have been important to budworm outbreaks in the 20th century. Notable outbreaks tended to occur during years of early springs with average air temperature, following winters with lower than average precipitation. Based on this finding, it is proposed that with high overwintering survival, increased population growth rates, and a longer growing season, the extent of future outbreaks will shift northward and may increase in size.

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1.0 Introduction

Knowledge of the natural disturbance history of forest ecosystems over broad temporal and spatial scales is essential for understanding forest dynamics (Pickett and White 1985). By studying the history of these disturbances, we can identify the trends, variations and periodicities of events and processes that are likely to sustain or change forest ecosystems (Wickman et al. 1994; Swetnam et al. 1999).

Insects are an integral component of forest ecosystems with important roles in forest dynamics (Haack and Byler 1993) and their action often interacts with other forest disturbances (ie. pathogens, fire, windthrow). For example, lodgepole pine trees weakened by butt rot fungus (*Polyporus schweinitzii* (Fr.:Fr.*)* are more easily attacked by the mountain pine beetle (*Dendroctonus ponderosae* (Hopkins)) (Parminter 1997). The subsequent accumulation of dead fuels increases the probability of forest fires that can create basal scars on the surviving trees, which are then infected by the fungus – and the process begins again (Parminter 1997). Conversely, the effects of one disturbance agent may delay another disturbance agent indirectly and for a limited time. For instance, the mountain pine beetle does not usually attack lodgepole pine forests regenerated after wildfire until 80 years or so have passed (Heath and Alfaro 1990; Safranyik et al. 2001). The continued interaction between mortality caused by mountain pine beetle and extensive wildfires, perpetuates lodgepole pine forests at a landscape level in some ecosystems.

Climatic variations, such as wet and dry episodes, may also increase or decrease the vulnerability of trees to insect attack (White 1976; Larsson 1989; Ryerson et al. 2003). It has been observed that the density of natural populations of a few lepidopteran species (ie. *Choristoneura*) increases during extended periods of warm dry weather (Campbell 1989). Attempts have been made to relate these observations to a change in the nutritive quality of the host plant foliage. For example, periods of water stress may cause a host plant's foliage to increase the concentration of minerals, soluble nitrogen and sugars (White 1976; Rhoades 1979; Clancy 1992). In contrast, Haukioja and Hakala (1975) argue that the accumulations of antagonistic secondary compounds are reduced during periods of water stress. Conversely, the observed response of lepidopteron populations to warm dry weather "may be explained by good weather promoting caterpillar feeding and warm and/or dry weather reducing insect disease" (Myers 1981:23).

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 (Alfaro and Maclauchlan 1992, Mason et al. 1997). The width of annual rings produced during the infestation years is progressively reduced with each additional year of defoliation, in a cause-effect relationship that usually has a one or more year lag (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. Because of its preferential feeding on the current year's buds and foliage, budworm reduces or eliminates apical growth during each year of defoliation. In addition, severe defoliation events that extend over a number of years often cause mortality of the upper crown in a type of damage known as die-back or top kill; this type of damage reduces the height of the tree by one to several internodes (Alfaro and Maclauchlan 1992). Trees that survive die-back resume height growth by means of lateral branches gaining apical dominance or by branches that originate from adventitious buds in the main stem (Van Sickle et al. 1983; Alfaro and Maclauchlan 1992).

The value of long-term ecological research is well recognized in ecology (Franklin and Forman 1987; Oliver 1990). This thesis provides an opportunity to assess the long-term interactions and effects between climate and radial growth in forest stands impacted by the western spruce budworm in a (IDF) landscape. The research was undertaken at study sites designated as part of the *Opax Mountain Silviculture Systems Research Project*. The Opax Mt. silvicultural systems site is a key research facility in the Southern Interior, providing an extensive set of treatments for long-term research. The information collected will provide insights into the effect of defoliation by western spruce budworm on radial growth at low elevation sites that have specific timber supply and restoration concerns that have not previously been addressed. It is anticipated that the findings will strengthen sustainable forest management practices for the region by providing insights into the range of natural variability of historical outbreaks that can be used to construct predictive models using outbreak and environmental parameters.

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

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 ten or more years (Brubaker and Greene 1979, Alfaro et al. 1982; Harris et al. 1985). Severe historical western spruce budworm infestations appear related to warm dry summers, when optimal synchrony between larval emergence and bud flush increase the vulnerability of Douglas-fir trees to attack by the western spruce budworm (Thomson et al. 1984). Impending climatic changes within interior British Columbia are predicted to lead to increasingly warmer and drier summers (British Columbia Ministry of Water, Land and Air Protection 2002) that are anticipated to increase the severity and frequency of significant western spruce budworm infestations over the next century (Williams and Liebhold 2000).

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. Prior to 1949 there was no prescribed sampling plan for estimating one-year cycle budworm populations and defoliation boundaries may not always have been reliably recorded (Harris et al. 1985).

The purpose of this research was to establish the history of budworm outbreaks in representative IDF stands near Kamloops, British Columbia (Fig. 1), and to document any relationships between historical western spruce budworm infestations and climatic variables. Standardized dendrochronological techniques were used to determine the magnitude and frequency of these events (e.g. Fritts 1976; Wickman et al. 1980; Zhang et al. 1999). Trees respond to climate, insect, fire, and other environmental disturbances with corresponding changes in their annual growth rings. Consequently, a disturbance record is retained in tree rings that can be examined using standardized dendroecological techniques (Fritts and Swetnam 1989).

The effects of *Choristoneura* sp. outbreaks on tree growth have been inferred by comparing tree-ring chronologies from host and non-host species (Alfaro et al. 1982; Kemp et al. 1985; Mason et al. 1997; Swetnam and Lynch 1993; Ryerson et al. 2003). In this study, host tree and non-host tree-ring chronologies were compared to the historical forest insect and climate station records to examine the relationship between climate and the onset and duration of western spruce budworm outbreaks (Swetnam et al. 1985; Swetnam and Lynch 1993; Swetnam et al. 1995; Swetnam et al. 1999; Ryerson et al 2003). It was anticipated that these findings would provide an opportunity to present a perspective of the likely response of western spruce budworm to impending climatic changes in the dry Douglas-fir forests of interior British Columbia.

Research Background

Across North America, episodic outbreaks of defoliating insects of the genus *Choristoneura* spp. have stimulated research aimed at understanding their biology and impact (Morris 1963; Ludwig et al. 1978; Wickman 1978; Blais 1983; MacLean 1984; Royama 1984; Sanders et al. 1985; Piene 1989; Shepherd 1992; Morin 1994; Bergeron et al. 1995; Krause 1997; MacLean and MacKinnon 1997; Mason et al. 1997; Parent et al.

2001). In the 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 of hosts are associated with density increases of 40% or more with respect to endemic levels. Outbreaks of this intensity are the result of improved reproduction and survival, or spread from other infested locations (Shepherd 1977; Campbell 1993).

Throughout its range, the western spruce budworm completes a single cycle of development from egg to adult within 12 months (Brookes et al. 1987). Moths emerge from pupal cases in late July or early August, and mate within 7 to 10 days, after which the female deposits her eggs and dies. Females deposit approximately 150 eggs each, usually on the underside of conifer needles (Shepherd 1977; Campbell 1993). Eggs hatch in the fall and the young larvae overwinter on the host tree in hibernacula among the leaves. In early May to late June, larvae leave their hibernacula to search for food. They first mine into year-old needles, closed buds, or newly developing vegetative or reproductive buds (Brookes et al. 1987; Campbell 1993). As new shoots flush, larvae spin loose webs among the needles and feed on the new foliage. As shoots continue to elongate and needles develop, adjacent shoots often are webbed together by the larvae and begin to appear twisted or stunted. New foliage is the preferred food and only after it is entirely consumed will the larvae feed on older needles. On some hosts, larvae favour developing male flowers and conelets as food, but on western larch larvae mine and sever the terminal and lateral shoots (Brookes et al. 1987).

There are two factors related to bud development that 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 time of development remaining for the insect 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, 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 to occur with other closely related species where flushing dates are important for the establishment of *C. fumiferana* (Clem), *C. conflictana* (Walker) *and C. rosaceana* (Harris) larvae.

Past outbreaks were the focus of intense entomological research through the Canada-USA Spruce Budworms Research Program (CANUSA) (Sanders et al. 1985). Before, during and after CANUSA several studies focused on the temporal and spatial impacts of budworm defoliation (Brubaker and Greene 1979; Alfaro et al. 1982; Kemp et al. 1985; Alfaro and MacLauchlan 1992). In the montane forests of Rocky Mountain National Park, western spruce budworm altered the stand structure by increasing mortality among defoliated understorey trees and predisposed host trees to subsequent pathogens (Stillwell 1956) and bark beetle attack (Hadley and Veblen 1993). The susceptibility of forests to budworm attacks is also believed to be related to the proportion of mature crown area, the availability of suitable food at specific times of larva development, and the proportion of Douglas-fir trees in the forest (Shepherd 1959;

Blais 1985; MacLean and MacKinnon 1997). During defoliation events this manifests itself as a reduction of the Douglas-fir component, a change in the host tree quality favouring tree resistance, and subsequently reduction in stand susceptibility to budworm defoliation (Underwood 1999; Awmack and Leather 2002).

Although there has been only limited research undertaken to examine the effect of climate on western spruce budworm infestations in the IDF forests of British Columbia (Wagg 1958, Shepherd 1961, Hard et al. 1980, Thomson et al. 1984), Thomson (1979) has emphasized the importance of climate on establishing a synchrony between larval emergence and bud flush. Similarly, Swetnam and Lynch (1993) noted a positive relationship between spring and early summer precipitation and the occurrence of regional-scale outbreaks in northern New Mexico. More recently, Ryerson et al. (2003) have also reported that western spruce budworm outbreaks in the mixed conifer forests of south-central Colorado State typically corresponded with times of increased moisture.

2.1 Materials and Methods

Study Area

Field investigations focused on forest stands located near Kamloops, British Columbia (50° 49' 31.2" N, 120° 28' 20" W) in the summer of 2001 (Fig. 1, Table 1). This region is characterized by mixed stands of Douglas-fir and ponderosa pine at low to mid elevations (400-1250 m asl) and Douglas-fir and lodgepole pine at high elevations (1130-1460 m asl). The understorey vegetation contains a moderate to high cover of pinegrass (*Calamagrostis rubescens* Buckl.), with lesser amounts of birch-leafed spirea (*Spiraea betulifolia* Dougl. ex Greene), heart-leafed arnica (*Arnica cordifolia* Hook.), soopolallie (*Shepherdia canadensis* (L.) Nutt.), falsebox (*Paxistima myrsinites* (Pursh)

Raf.), twinflower (*Linnaea borealis* L.) and kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng.) (Lloyd et al. 1990 ; Parish et al. 1996). Dry sites have an open canopy of Douglas-fir, with an understorey dominated by bluebunch wheatgrass (*Agropyron spicatum* (Pursh.) A. Löve), junegrass (*Koeleria macrantha* Ledeb.), fescues (*Festuca* spp. L.) and lesser amounts of snowberry (*Symphoricarpos albus* (L.) Blake) and Saskatoon berry (*Amelanchier alnifolia* Nutt.) (Lloyd et al. 1990; Parish et al. 1996). Similar IDF zones extend south into Washington, Oregon, Idaho and Montana (Lloyd et al. 1990; Parish et al. 1996).

Forest Insect and Disease Survey (FIDS) records for the study area indicate that between 1954 and 1963 the one-year cycle budworm was present only in low numbers. In the interval from 1964 to 1982 no budworms were detected nor was any defoliation seen in the study area. Beginning in 1983 and continuing through to 1992, populations of budworm increased to outbreak levels, with defoliation intensities ranging from light to severe. From 1994 through to 2000 no defoliation to low defoliation levels were detected by either aerial or ground surveys (Erickson 1987; Koot and Hodge 1995; BC Ministry of Forests 2001).

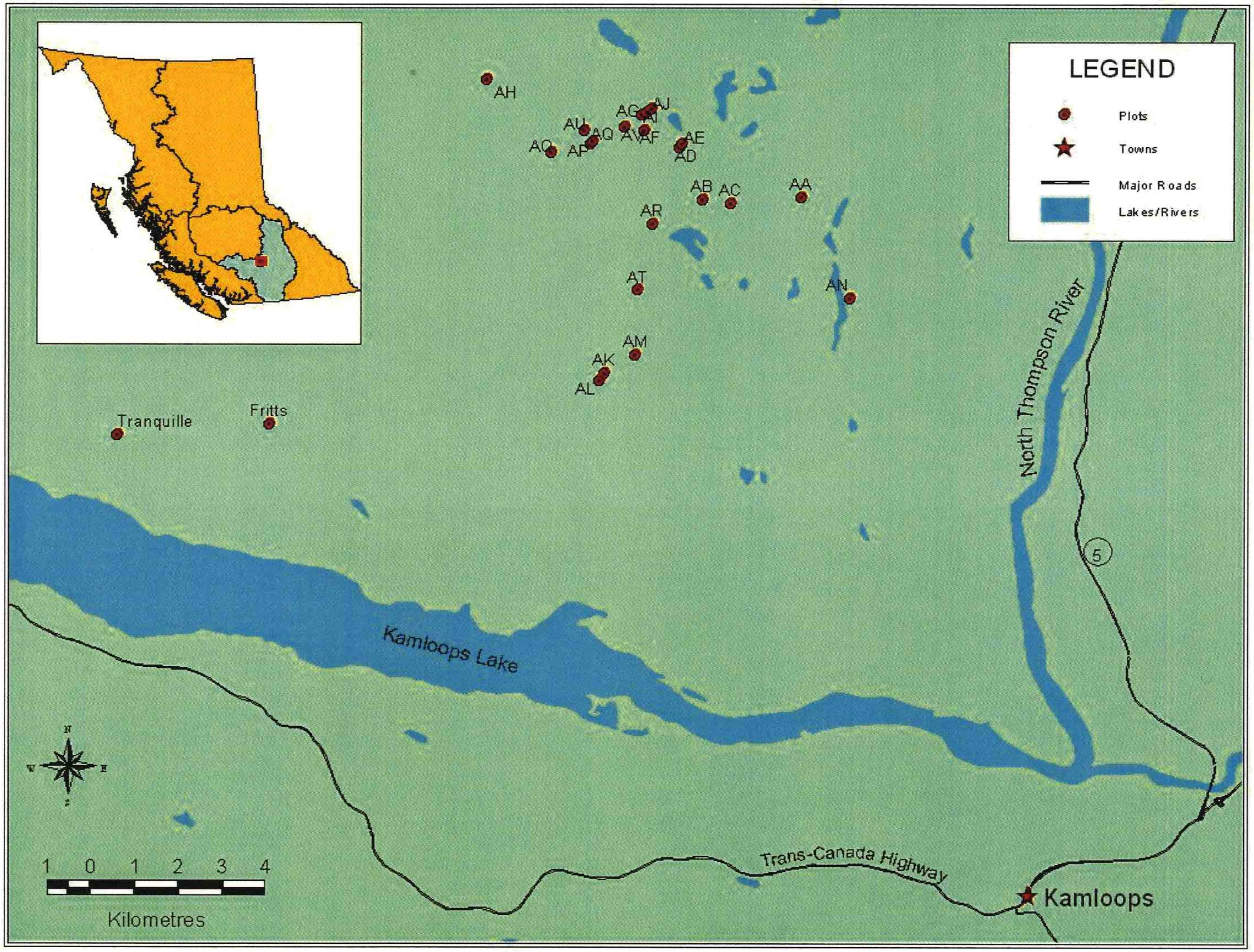


Fig. 1. Map of Kamloops Forest Region, showing locations of Douglas-fir and ponderosa pine stands sampled in this study.

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

Location	Site	Species	Latitude	Longitude-W	Elevation (m)	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[b]	PP	50° 46’	120° 39’	850	S
	Fritts[b]	PP	50° 46’	120° 36’	700	NW

[b] Chronology provided by E. Watson (Watson and Luckman 2002)

For this study, twenty mixed stands of Douglas-fir and ponderosa pine (non-host) trees were selected from within a 325 km^2 area of documented historic defoliation (defoliated crown) (Erickson 1987; Koot and Hodge 1995). Increment borers were used to extract two cores per tree at DBH (1.3 m above the ground), to the pith, for a minimum of 20 trees per site for a total of 284 Douglas-fir. Ponderosa pine trees (65) were selected from nearby but separate stands. Individual trees were selected based on their DBH (> 42.0 cm) and the presence of crown defoliation.

All 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 the annual ring increments to the nearest 0.01 mm. The measured ring sequences were visually cross-dated by identifying key ring-width features (Stokes and Smiley 1968; Swetnam et al. 1985) and quality checked using the International Tree-Ring Data Bank (ITRDB) software program COFECHA (Holmes et al.1986; Holmes 1994). In this instance, verification was based on 50-year dated segments with a 25-year lag, at a 99% critical level of correlation of 0.32 (Fritts 1976). Segments that did not cross-date were deleted or corrected until a significant correlation was obtained for all site chronologies.

A double de-trending procedure within the computer program ARSTAN (Holmes et al. 1986) was used to produce a standardized ring-width index series. 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 (ie. insects and climate). Standardization was accomplished by fitting flexible curves (cubic splines) to each measured ring-width series and then dividing the ring-width values by the value of the fitted curve to produce tree-ring indices. The ring width series were standardized with a combination of two frequency response cubic splines (50% frequency response, with 100 yr minimum lengths and 67% rigidity, minimum rigidity 32 years) (Cook and Peters 1981; Cook and Holmes 1986; Cook and Kairiukstis 1990). All of the cross-dated, de-trended Douglas-fir indices were averaged into site chronologies using a bi-weight robust mean (Cook and Holmes 1986).

A regional ponderosa pine chronology was constructed by combining cross-dated cores collected within the study area with those previously collected in Tranquille Valley by Watson and Luckman (2001, 2002)(Fig. 2). The combined chronology spans the interval from 1523-2000 AD and has a mean inter-serial correlation of 0.63 (Table 2). A mean sensitivity value of 0.32 indicates that the trees should have good dendroclimatic utility (Fritts 1976).

A regional Douglas-fir chronology was constructed by combining cross-dated cores collected within the study area. This chronology spans the interval from 1600-2000 AD and has a mean inter-serial correlation of 0.56 (Table 2) (Fig. 3). A mean sensitivity value of 0.27 indicates that the trees should have good dendroclimatic utility (Fritts 1976).

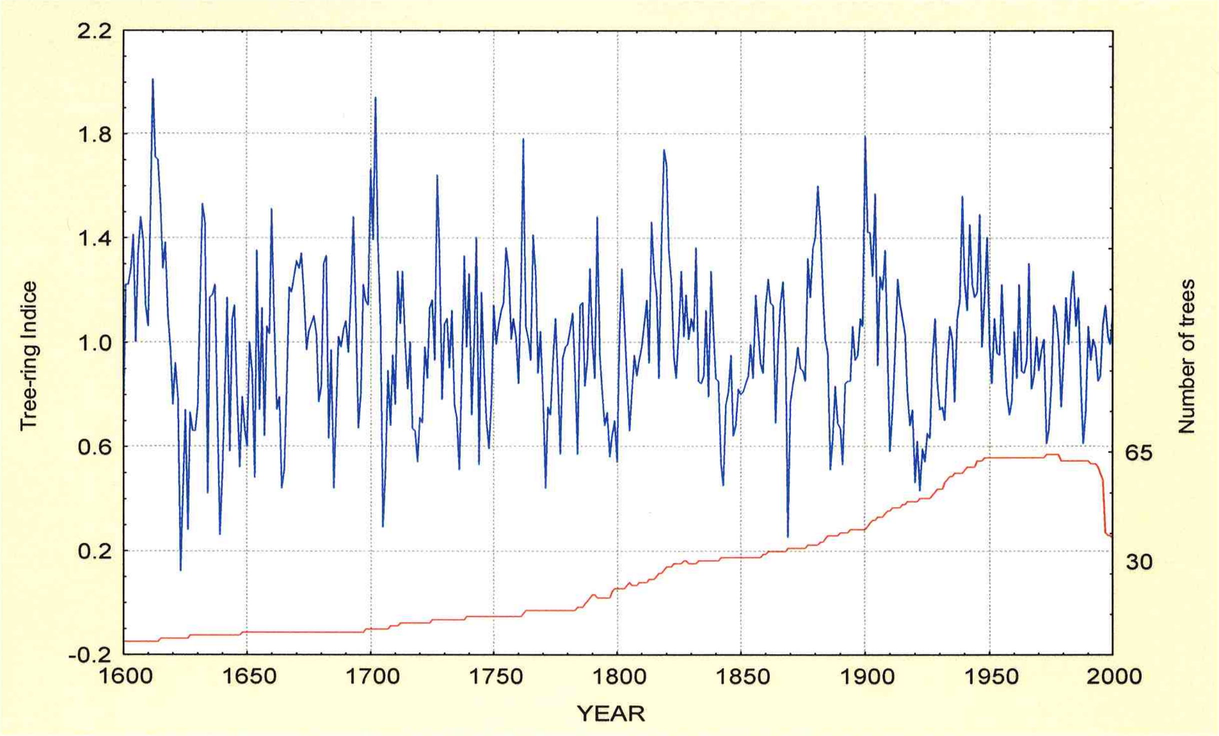


Figure 2. Master chronology (top) of ponderosa pine near Kamloops, British Columbia, 1600-2000 and number of trees contributing to each year of the chronology (bottom) (n=65 trees).

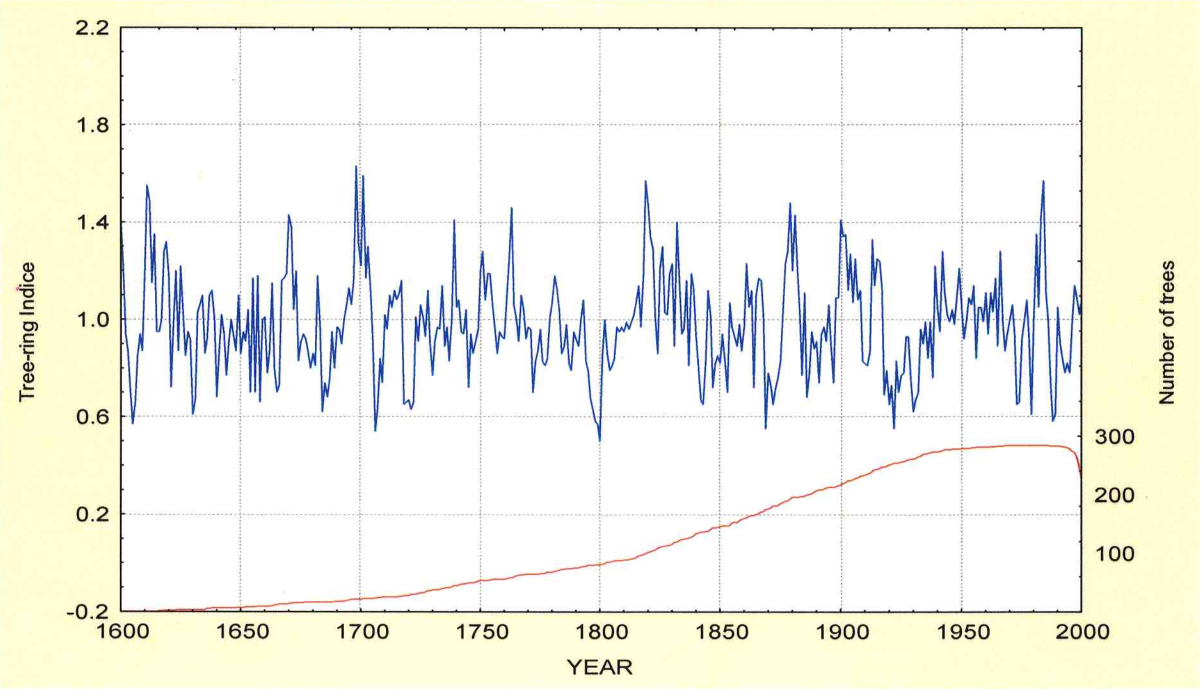


Figure 3. Master chronology (top) of Douglas-fir near Kamloops, British Columbia, 1600-2000 and number of trees contributing to each year of the chronology (bottom) (n=284 trees).

Outbreak reconstruction

Cores 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 infer past outbreak occurrences throughout individual tree-ring chronologies by assigning values to parameters in the software program OUTBREAK Version 6.00P (Holmes and Swetnam 1996). OUTBREAK automates the correction of host tree-ring chronologies (all site standardized ring-width series averaged per site) and applies a set of user-defined criteria for the identification of possible insect outbreaks periods and related growth reduction, duration, percentage maximum annual growth reduction, and percentage mean periodic growth reduction for each outbreak in each tree chronology (Swetnam et al. 1995; Speer et al. 2001; Ryerson et al. 2003). In this instance, parameters were established that adequately represented the general pattern of magnitude and duration of reduced growth observed in the tree-ring series during the known 20th-century outbreaks. Specifically, a minimum threshold was set whereby a minimum of 8 years of below average growth and a growth reduction in at least one year below -1.28 std. dev. 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 increased radial growth year when larval populations may have temporally declined before surging. To differentiate between an outbreak event and incipient events (or background noise), duration and growth reduction were summarized for periods at each site for outbreaks with 30% or more trees recording a reduction in growth. The duration and quantity of growth reduction for the trees showing outbreaks were averaged together by site.

Climate and the seasonal timing of infestation are also factors that need to be considered in dendroecological reconstructions of insect outbreaks (Fritts 1976, 1991). Previous investigations have shown that Douglas-fir and ponderosa pine growing in comparable sites tend to have similar radial growth responses to climate (Fritts 1974). To eliminate these 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. 1985, 1995). The "corrected" indices were calculated with the following equation:

$$[1] \qquad \text{Corrected index} = I_{ht} - \frac{SD_h}{SD_n}\left(I_{nt} - \bar{I}_n\right)$$

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

"Corrected" indices serve as records of radial growth in the host tree after reduction or elimination of climate signals as indicated by the non-host. The year of maximum growth reduction for each outbreak was defined 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 (or potential growth) in standardized ratio indices. Values less than 1.0 in the 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. A regional time series of outbreaks was computed by summing the numbers of trees recording an outbreak 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 recording outbreaks in each year. This procedure was done by dividing the number of trees recording outbreaks each year by the total number of trees with measurements for that year, and then multiplying by 100.

The timing of the infestation periods identified by OUTBREAK was verified by scrutinizing the dated tree-ring specimens and comparing with confirmed historical defoliation episodes from Forest Insect and Disease Survey (FIDS) and British Columbia Ministry of Forests aerial survey records (Erickson 1987; Koot and Hodge 1995; British Columbia Ministry of Forests 2001). Although an annual history of forest insect infestation in the Kamloops Forest Region extends back to 1912, continuous and reliable records of estimated defoliated areas in the region for western spruce budworm are limited prior to 1969 (Koot and Hodge 1995).

Response function analysis was used to define the radial-growth response of the regional Douglas-fir and ponderosa pine tree ring chronologies to precipitation and temperature conditions (PRECON 32, Version 5.17B, 1999) recorded at Kamloops, British Columbia from 1895 – 1998 (http://www.cccma.bc.ec.gc.ca/hccd/data/access_data.html).

These variables were used to recalculate matrices of climatic data using principal components analysis to form new orthogonal variables that maximized the variance in the monthly climate parameters. The new orthogonal variables were then regressed with master tree ring chronologies for Douglas-fir and ponderosa pine (Fritts et al. 1979). Each orthogonal variable explains successively lesser amounts of variance in the tree ring record (Guiot et al. 1982). Predictor variables were then tested using a bootstrap method in PRECON 32 (Efron 1979; Guiot 1991), which constructed a probability distribution for each chronology. The end result of this process was such that greater confidence could be placed in the predictor variables driving radial-growth than if no cross-validation is carried out (Guiot 1990, 1991).

PRECON 32 was used to identify which significant regression coefficients were related to monthly climate parameters. A matrix of significant variables was multiplied by the principal component scores (constructed from the initial input variables and their eigenvector loadings), to express the significant regression coefficients into a new set of terms expressed in original climate variables rather than principal components. The output from PRECON 32 graphically represented the significant initial climate variables as response functions that demonstrated the calculated relationship between the monthly climate variables and radial growth (Fritts et al. 1991).

Relationships between western spruce budworm outbreaks and climate were analyzed by comparing the regional outbreak series with precipitation and temperature data divided into: winter (Nov. - Feb.), spring (Mar. – Jun.), and summer (Jul. – Oct.) monthly mean temperature and total monthly precipitation variables. The coincidence of budworm outbreak periods (in the regional budworm series) and wet-dry periods in the precipitation record were examined using stepwise regression analysis.

A linear regression model was developed to predict ponderosa pine ring-width growth during years of outbreak based on the percentage of Douglas-fir trees affected by western spruce budworm in a site (Transfor), June temperature (June T), March precipitation (March P), August precipitation and the seasonal variable winter precipitation (November, December, January)(Winterp). An arcsine transformation was performed on the percentage of Douglas-fir trees attacked by western spruce budworm, in order to meet the assumption of normality.

2.2 Results

Dendrochronological findings

A total of nineteen Douglas-fir (284 trees, 568 cores) site chronologies and a single regional ponderosa pine (65 trees, 130 cores) chronology were developed. 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 (Table 1, Fig. 1). The mean inter-serial correlation, describing the average pairwise correlations within each of the nineteen de-trended Douglas-fir site 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 (MS) describes the interannual variability in ring-widths as a proportion of the local mean ring width. In the case of Douglas-fir, the MS 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.

Table 2. Site and master chronology length, inter-serial correlation and mean sensitivity for Douglas-fir in nineteen sites near Kamloops, British Columbia used to study outbreak patterns of the western spruce budworm. Autocorrelation describes the growth in any given years as it relates to growth in previous years. Correlation coefficients identify the strength of the relationship between the regional ponderosa pine chronology and each Douglas-fir site chronology.

Site[a]	Chronology length	Years	Inter-serial correlation	Number trees cored	Mean sensitivity	Autocorrelation	Correlation coefficients[b]
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[c]	1523-2001	478	0.63	65	0.32	0.72	
Douglas-fir	1600-2000	400	0.56	264	0.27	0.74	

[a] For site identifiers see Table 1.

[b] Correlation of ponderosa pine with Douglas-fir.

[c] Portion of pine chronology provided by E. Watson (Watson and Luckman 2002)

All nineteen Douglas-fir site chronologies were significantly correlated ($p<0.05$) with the regional ponderosa pine chronology over the period from 1600 to 2000 AD. Correlation coefficients ranged from 0.32 to 0.72 (Table 2). These findings suggest that the Douglas-fir chronologies within the IDF contain a common radial growth signal, which Watson and Luckman (2001, 2002) previously attributed to regional climate conditions. Cores contributing to the Douglas-fir regional chronology span the interval from 1600 to 2000 AD (mean inter-serial correlation 0.56, mean sensitivity 0.27; mean autocorrelation 0.74; Table 2).

Frequency of Outbreaks

Seven outbreak events were distinguished over the last 300 years of the tree-ring record (starting in the early 1700s, 1720s, mid 1750s, 1780s through to the early 1800s, late 1890s, 1930s, 1985) in the localities studied (Fig. 4). Inferred historical outbreaks in the late 1890s, early 1800s and mid 1720s occurred in 63%, 39% and 60% of the stands respectively (Table 3) (Fig. 5). While confidence in reconstructing possible western spruce budworm outbreaks prior to the early 1700s declines as the number of chronologies in the sample decreases, the data indicate that outbreaks in the study area occur on average every 43 years after the early 1700s.

Historical records were examined to confirm the most recent defoliation events identified by OUTBREAK (Fig. 4). Although the reconstruction indicates that a defoliation event occurred in the 1930s at 82% of the sites (Fig. 4), this event was not documented in the FIDS records (1912-2000 AD). Between 1985-1995, western spruce budworm outbreaks were confirmed at 60% of our sites and all of them appear in the

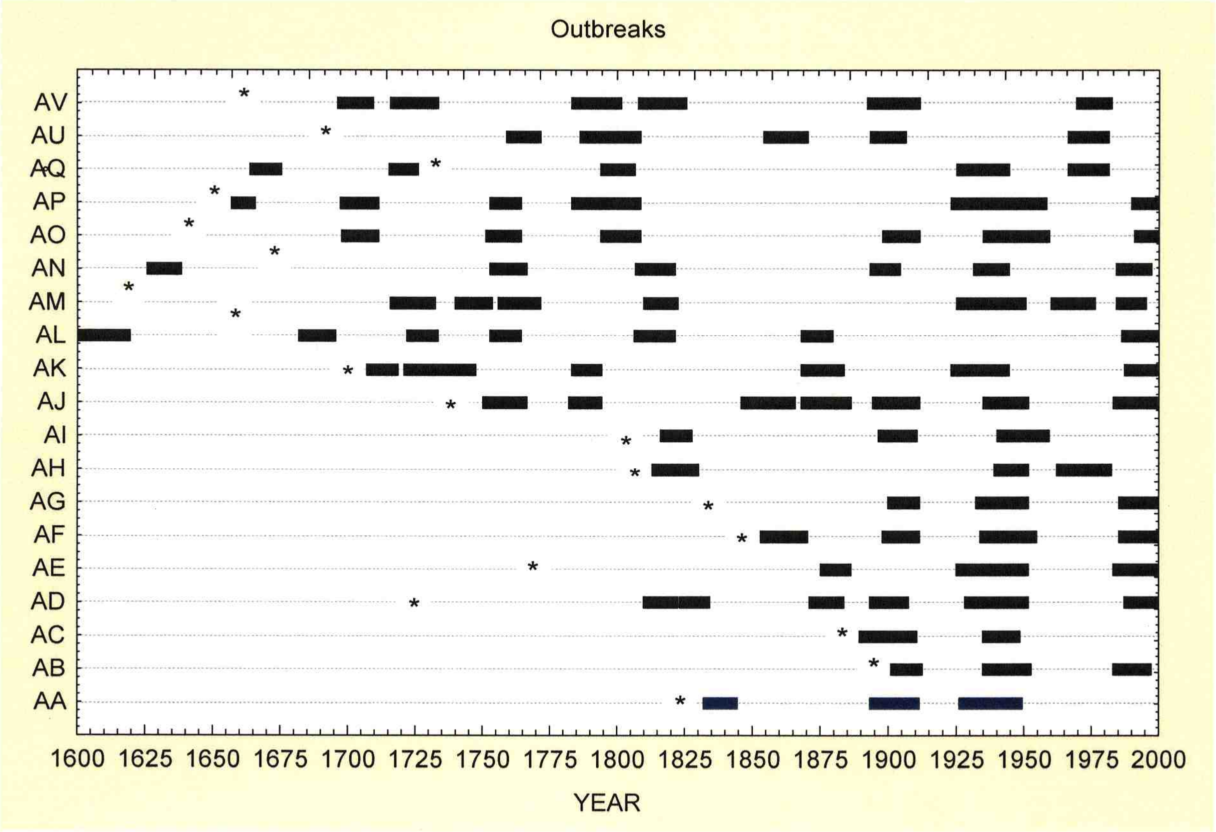


Figure 4. Periods of reduced growth relative to ponderosa pine, which indicate potential western spruce budworm outbreak timing and duration in interior Douglas-fir forests near Kamloops, British Columbia from 1600-2000. Duration of infestations (black bars) inferred from Douglas-fir trees chronologies for each stand. Beginning of chronologies indicated by *.

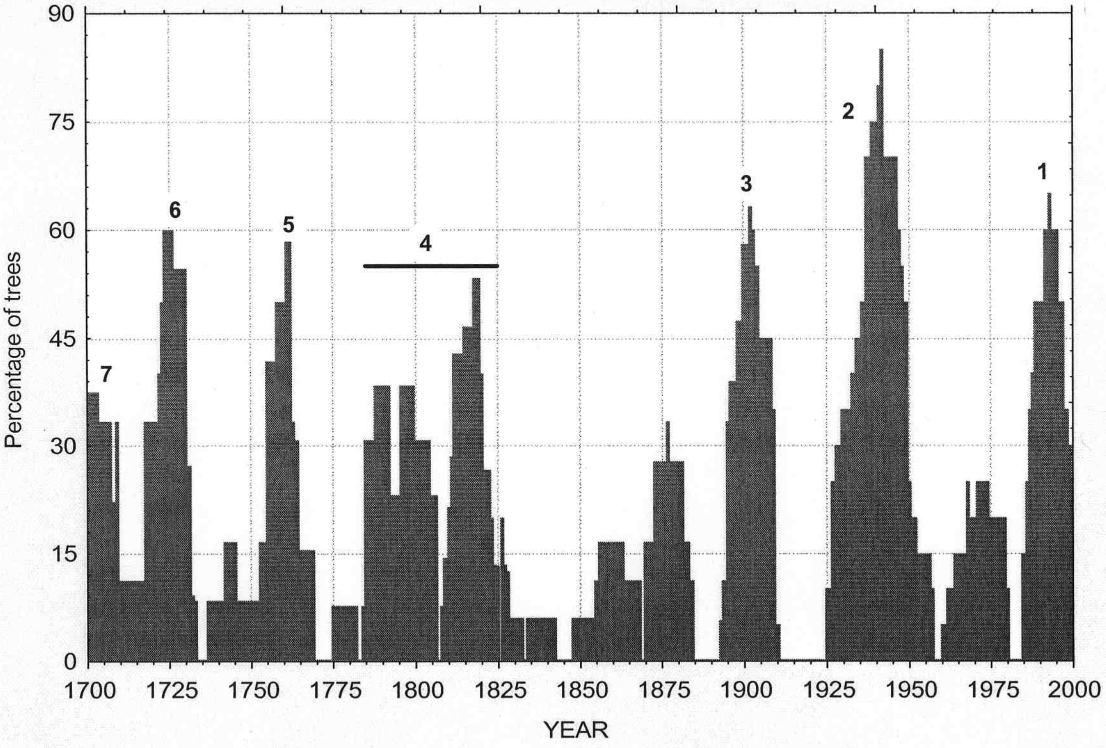


Figure 5. Percentage of Douglas-fir trees with reduced growth relative to ponderosa pine. A minimum of ≥ 30% of trees in a given year must demonstrate reduced growth to be classified as having had a western spruce budworm outbreak. Seven outbreaks were identified in the study area.

Table 3. Dates of inferred outbreaks, duration of growth reduction, interval between previous reduced growth (years), periodic growth reduction as compared to ponderosa pine and maximum reduction in Douglas-fir during inferred outbreaks of western spruce budworm, near Kamloops, British Columbia.

Site	Dates	Duration of growth reduction (years)	Interval (# of years)	Periodic growth reduction (%)	Maximum growth reduction (%)	Year of Smallest ring
AA	1834-1842	9	---	13.8	49.7	1836
	1895-1909	15	53	25.4	53.4	1892
	1928-1947	20	19	22.6	51.9	1934
AB	1903-1919	8	---	41.2	70.5	1906
	1937-1950	14	18	22.8	53.9	1938
	1989-1995	11	39	25.1	63.0	1985
AC	1898-1908	11	---	37.9	81.9	1906
	1937-1946	10	29	19.4	38.4	1937
AD	1812-1820	9	---	24.6	73.5	1818
	1825-1832	8	5	9.1	43.2	1832
	1873-1881	9	41	18.9	41.2	1881
	1895-1904	10	14	13.0	49.9	1906
	1930-1949	20	26	23.5	81.7	1939
	1989-1999	11	40	19.3	52.7	1990
AE	1877-1884	8	---	18.2	35.5	1880
	1927-1949	23	43	21.2	63.3	1938
	1985-1997	13	36	24.2	47.4	1986
AF	1855-1868	14	---	16.8	44.9	1856
	1900-1909	10	32	12.8	27.9	1900
	1936-1952	17	27	17.8	51.5	1938
	1987-2001	15	35	15.4	45.6	2001
AG	1902-1909	8	---	11.5	34.4	1900
	1934-1949	16	25	27.4	60.5	1938
	1987-2001	15	38	21.1	100.0	2001
AH	1815-1828	14	---	36.9	94.5	1818
	1941-1949	9	113	4.6	32.5	1946
	1964-1980	17	15	21.6	50.1	1965
AI	1818-1825	8	---	52.3	100.0	1819
	1898-1908	11	73	17.5	55.4	1900
	1942-1957	16	34	14.9	39.7	1946
AJ	1752-1764	13	---	31.3	100.0	1766
	1784-1792	9	20	16.9	57.5	1792
	1848-1863	16	56	34.1	83.0	1850
	1870-1884	15	7	21.9	43.9	1870
	1896-1909	14	12	12.4	47.8	1900
	1937-1949	13	28	24.5	56.5	1938
	1985-1997	13	36	17.1	44.0	1985

AK	1709-1716	8	---	26.6	70.5	1709
	1723-1733	11	7	17.4	100.0	1727
	1737-1745	9	4	6.9	50.5	1745
	1785-1792	8	40	19.6	61.9	1785
	1870-1881	12	78	18.3	43.8	1870
	1925-1942	18	44	19.0	75.0	1942
	1989-1997	9	47	24.3	62.6	1990
AL	1602-1617	16	---	30.5	61.5	1602
	1684-1693	10	67	21.1	45.3	1672
	1724-1731	8	31	20.8	63.8	1727
	1755-1762	8	24	16.6	43.0	1762
	1808-1819	12	46	12.3	44.4	1814
	1870-1877	8	51	19.9	35.3	1877
	1988-1998	11	111	17.4	40.1	1992
AM	1718-1730	13	---	13.6	37.7	1725
	1742-1751	10	12	18.3	45.1	1745
	1758-1769	12	7	12.7	30.9	1761
	1812-1820	9	43	9.34	34.5	1814
	1927-1948	22	107	15.2	35.3	1938
	1962-1974	13	13	11.2	45.5	1976
	1986-1993	8	12	25.0	40.5	1986
AN	1628-1636	9	---	14.9	59.9	1635
	1755-1764	10	119	13.2	74.2	1764
	1809-1819	11	45	21.4	59.5	1818
	1895-1902	8	76	21.0	81.3	1904
	1933-1942	10	31	26.1	83.1	1939
	1986-1995	10	44	25.5	68.4	1983
AO	1700-1709	10	---	23.9	79.4	1702
	1753-1762	10	44	15.7	55.8	1762
	1796-1806	11	34	13.5	41.4	1806
	1900-1909	10	94	19.3	44.8	1900
	1937-1957	21	28	28.8	57.5	1946
	1993-2000	8	36	23.2	39.7	1993
AP	1654-1663	10	---	6.1	68.2	1660
	1699-1709	11	36	20.5	65.3	1702
	1755-1762	8	46	10.4	35.0	1762
	1785-1806	22	23	16.7	41.9	1785
	1925-1956	32	119	19.7	62.7	1946
	1992-2001	10	36	23.6	71.3	2001
AQ	1666-1673	8	---	19.8	61.6	1667
	1717-1730	14	44	13.3	47.9	1727
	1796-1804	9	66	15.5	38.0	1792
	1927-1942	16	123	12.5	42.7	1938
	1968-1979	12	26	12.1	29.2	1968

AU	1761-1769	9	---	12.1	54.6	1766
	1788-1806	19	19	23.7	78.3	1801
	1856-1868	13	50	17.8	33.1	1856
	1895-1904	10	27	17.8	48.6	1904
	1968-1979	12	64	20.4	45.1	1976
AV	1698-1707	10	---	22.7	71.9	1700
	1718-1731	14	11	15.5	54.3	1727
	1785-1799	15	54	13.2	44.6	1792
	1810-1823	14	11	23.7	59.0	1814
	1894-1909	16	71	17.5	46.3	1904
	1971-1980	10	62	12.8	31.5	1968

tree rings within one to two years of their recorded occurrence within local forestry reports (Koot and Hodge, 1995). 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 growth reduction limits the temporal precision of our outbreak reconstructions 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.

Relationship between budworm outbreaks and climate

Analyses of the Kamloops climate record revealed that a weak relationship exists between total seasonal precipitation and the mean annual air temperature (i.e. lower precipitation corresponded to higher temperatures) (Fig. 6). Between 1895 to 1998 annual precipitation totals averaged 302 mm/yr and the mean annual temperature was 8.4°C. During the two outbreak periods recorded in the 20th Century (1930s and mid 1980's), the annual precipitation totals dropped to below 200 mm/yr and the mean annual temperatures exceeded the long-term average by 0.6°C (1930s) and 2.1°C (mid 1980s).

The radial growth response of Douglas-fir and ponderosa pine to monthly mean air temperature and monthly total precipitation for the interval 1895-1998 are presented as response functions in Figure 7. The response functions for Douglas-fir indicate that 34.6% of the inter-annual variation in radial growth can be attributed to climate (Fig. 7). Radial growth of Douglas-fir was significantly and positively correlated to both precipitation in August of the growth year and to November and January

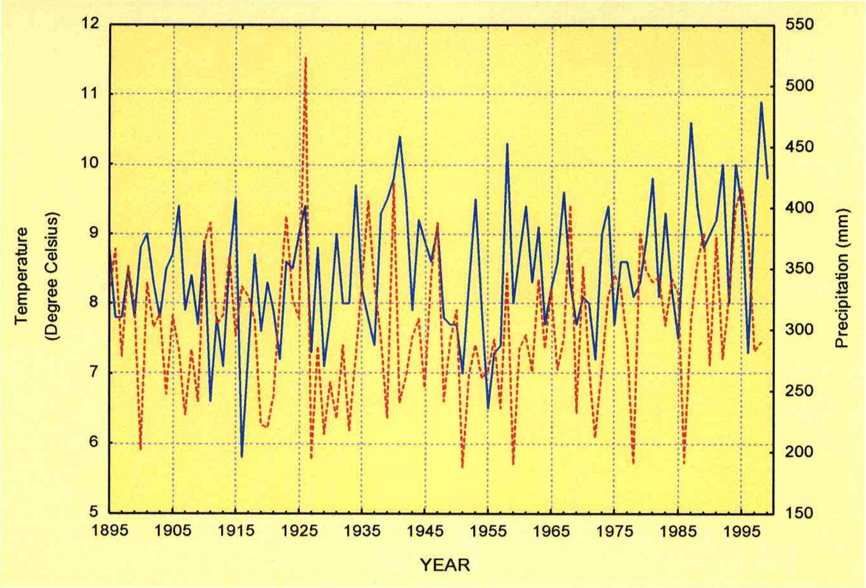
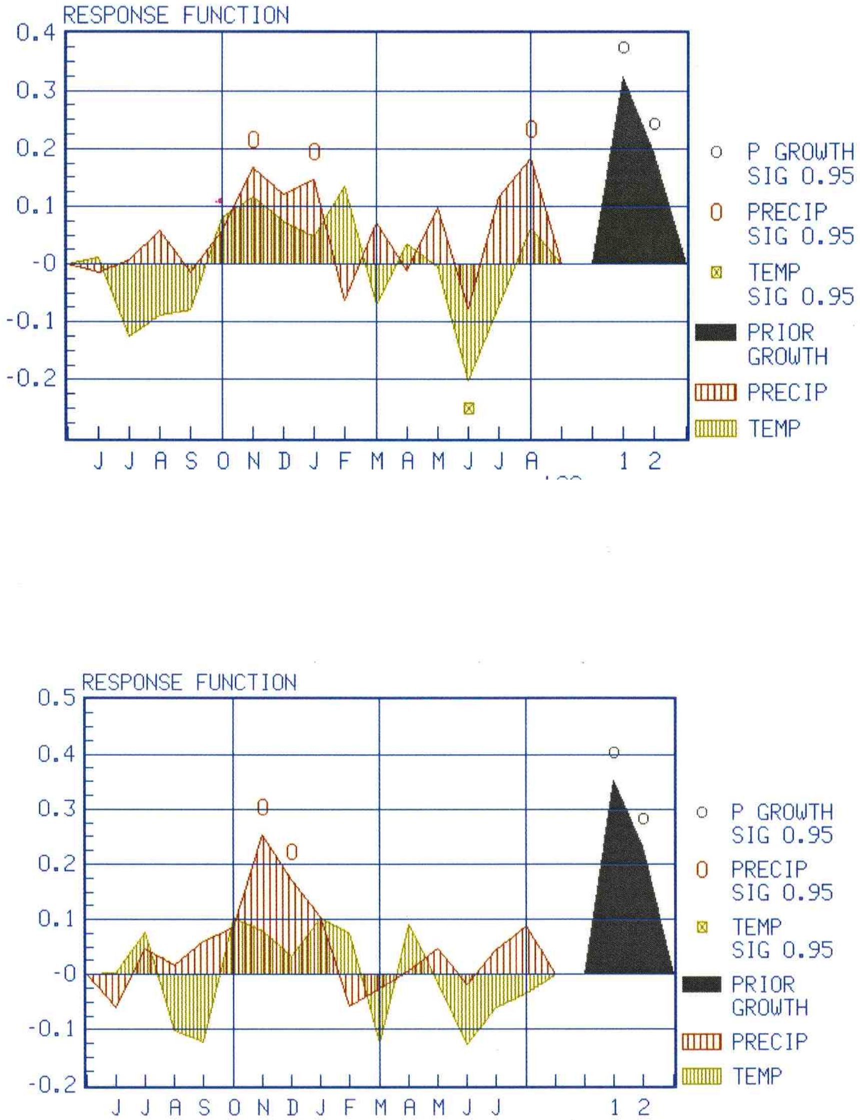


Figure 6. Climate for the study area averaged for A.D. 1895-1998 using precipitation (--) and temperature (°C) (—) records from the weather station at Kamloops, British Columbia.



b.

Figure 7. Response functions for Douglas-fir (a) and ponderosa pine (b) site tree-ring chronologies using weather data from Kamloops. Monthly climate interval variables for the interval A.D. 1895-1998 are used to explain the variance in tree rings. The labelled points (O – precipitation; ☒ temperature) represent a significant (95% level) effect of either temperature (green) or precipitation (red) on growth.

precipitation in the previous winter. Significant negative correlations with June air temperatures indicate that warmer than average conditions limit the magnitude of radial growth.

The response functions calculated for ponderosa pine indicate that 32.5 % of the inter-annual variation in radial growth can be attributed to climate (Fig. 7). Ring growth of ponderosa pine was significantly and positively correlated with November and December precipitation for the prior year; and negatively correlated with temperature in August and September of the prior year and June of the growth year.

A linear regression model was developed to predict ponderosa pine ring-width growth during known periods of western spruce budworm outbreaks. Ponderosa pine growth was significantly influenced by the collective effects of outbreak levels of western spruce budworm in the forest stand, June temperature, March precipitation, August precipitation and winter precipitation, as expressed in the regression model where, collectively, these variables yield an r^2 of 0.40. The model indicates that ponderosa pine ring-width growth increases when the Douglas-fir trees in the stand are being affected by western spruce budworm and decreases with lower than average precipitation in March, August and winter (November, December, January, February (NDJF) months. The elimination method was used to select variables for inclusion in the model, which was expressed as follows:

$$\text{Pine} = \beta_0 + \beta_1\text{Transfor} - \beta_2\text{JuneT} - \beta_3\text{MarP} - \beta_4\text{AugP} - \beta_5\text{Winterp}. \text{ (Table 4)}$$

Table 4. Parameter estimates and associated statistics for predicting growth of ponderosa pine in Douglas-fir forest affected by western spruce budworm near Kamloops, B.C. (site (Transfor), June temperature (June T), March precipitation (March P), August precipitation and the seasonal variable winter precipitation (November, December, January)(Winterp).

Independent Variable	Unstandardized coefficient	S.E.	*t*	p
Transfor	.529	.0791	5.763	>0.000
June T	-.22	.0806	-3.397	>0.000
Mar P	-.22	.0833	-2.789	>0.006
Aug P	-.24	.0837	-3.488	>0.000
Winter P	-.20	.0803	-2.757	>0.006

2.3 Discussion

Interpretation of the spatial and temporal impact of historical western spruce budworm defoliation events over the last three centuries are limited by the lack of direct observational data and the sensitivity of tree rings to varied degrees of defoliation. Nevertheless, the persistent absence of any reduction in the radial growth of ponderosa pine trees during known defoliation events provides some confidence that OUTBREAK does provide an objective means for identifying western spruce budworm defoliation events (Swetnam and Lynch 1993).

Seven regional, western spruce budworm population outbreaks at approximately 43-year intervals were identified in the Douglas-fir tree-ring record. The temporal synchrony of these outbreaks is similar to that of reports for *Choristoneura* species that are known to undergo population oscillations at scales of 13-35 years (Myers 1998; Swetnam and Lynch 1993; Williams and Liebhold, 2000; Ryerson et al. 2003). Moran (1953) suggests that a strong environmental cue could possibly act to spatial synchronize populations that are oscillating at different densities over the landscape. This requires no assumptions about the periodicity of weather patterns, but does require that insect populations be exposed to a common endogenous factor that can coordinate their oscillations. Spatial synchrony in annual precipitation and mean temperature are both significant and measurable over large geographic regions (Koenig 2002). However, this does not demonstrate causality, but rather suggests that environmental cues are capable of having a synchronizing effect on faunal populations. Given that climate directly and indirectly influences IDF forest dynamics it may be that extrinsic factors related to large-scale climate may play a critical role in synchronizing western spruce budworm population dynamics.

Tree-ring data from climatically-sensitive non-host ponderosa pine and host Douglas-fir are especially useful in studying long-term insect outbreak patterns because they provide replicated observations of past outbreaks in the context of ongoing climatic fluctuations (Swetnam and Lynch 1993; Ryerson et al. 2003). The occurrence of western spruce budworm outbreaks in the 1930s and mid 1980s occurred during periods of low winter precipitation as deduced from the ponderosa pine chronology. This suggestion is supported the findings of Thomson et al. (1984) who note that there exists a negative relationship between precipitation and severe western spruce budworm infestations. In a study conducted by Campbell (1989), he suggested that western spruce budworm larva fed on foliage collected during early spring seasons were 20% heavier and had a 25% difference in fecundity rates as compared to those fed on collections done during late spring seasons. This would suggest that the annual variations in spring climate affect the nutritive quality of foliage. Positive correlations of growth for both Douglas-fir and ponderosa pine with precipitation in winter (NDJF) prior to the growing season suggest that non-growing season precipitation is more important than growing season precipitation. An early spring season characterized by low precipitation during winter months and normal spring air temperature act as cues for the budworm to emerge (Perry and Pitman 1996). In contrast, bud-flush in Douglas-fir is dependent on both root temperature as well as air temperature (Shepherd 1992). Beckwith and Burnell (1982) found that in north central Washington State, climatic conditions in spring were such (warm air temperatures over deep snow packs keeping ground temperatures low) that budworm emerged before buds began swelling. Under these circumstances, western spruce budworm was forced to feed on older foliage or seek a new host, either of which results in high budworm mortality. Comparison of the outbreak chronology (not shown) and climate showed a strong positive relationship between winter (NDJF) precipitation and outbreak occurrence. Trees stressed by environmental factors, in particular drought, are less able to synthesize the necessary defence chemicals (Perry and Pitman 1996). Both tree species also showed negative correlations between growth and high summer temperatures. This finding suggests that increased evapotransportation and water loss induced by high temperatures reduced the radial growth of these species. The positive effect of spring precipitation on the radial growth of Douglas-fir suggested that water availability during the growing season is one limiting factor for radial growth of Douglas-fir, an observation consistent with information from other regions (Zhang et al. 1999). The positive effect of high, late fall temperature and precipitation on ring-width growth of Douglas-fir suggested that warm and moist days in late fall favour active photosynthesis and continuous food storage, leading to large ring-width in the following year (Fritts 1976; Waring and Franklin 1979).

3.0 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 examination of insect signatures within the tree rings of long-lived stands of Douglas-fir that sustained approximately 7 regional outbreaks over a period of three centuries. The existence of this historical record indicates that some overstorey trees can coexist with budworms for long periods of time. This behaviour is similar to that found by previous researchers (Swetnam and Lynch 1993; Swetnam et al. 1995; Alfaro et al. 2001; Ryerson et al. 2003) and appears to occur even when western spruce budworm populations do not reach the same level of defoliation in all trees (Myers 1993; Bjørnstad 2000). It is suspected that forest characteristics, such as the nutritive value of foliage, may be a factor preconditioning western spruce budworm populations success and that the regional climate has a synchronizing influence (Royama 1984; Shepherd 1985; Williams and Liebhold 1995, 2000; Myers 1998).

This study suggests that an early spring season characterized by low precipitation during winter months and normal spring air temperature increase the success of budworm emergence and reduce the Douglas-fir trees ability to defend against western spruce budworm foraging. Research conducted by Kemp (1986) reported that, during an infestation period of western spruce budworm, defoliation following an early spring was severe, whereas that following a late spring was only light to moderate. Myers (1981) has indicated that warm dry weather, which is characteristic of early springs, would promote caterpillar feeding and reduce the incidence of disease. Evidently spring climate can effect changes in both the host plants and the phytophagous species, which synergistically affect growth and survival of the phytophagous population; for example, early spring climates that promote budworm feeding and reduce disease and late spring climates suppressing the growth of the insect population (Myers 1981). This indicates that with higher over wintering survival, increased population growth rates, and a longer growing season, outbreak areas of some species are likely to shift in latitudinal range and may increase in size. Changes in geographical ranges and spatial extent of outbreaks of western spruce budworm are likely consequences of climatic change.

"Natural trajectory experiments", such as those of tree-ring reconstructions, can encompass large spatial scales (Diamond 1986). Thus, the strength of this historical-regional approach is that observations match the temporal and spatial scales of important processes influencing the system (Ricklefs 1987). Limitations of this approach include the lack of control of some of the interacting variables (ie. biotic, abiotic factors, other trophic levels). The tree-ring record is also inherently "noisy", and diminishing sample sizes with increasing time before present lowers the reliability of estimates in earlier periods. These problems prevent precise identification of the specific manner in which climatic variations influence budworm populations. Future research involving simultaneous observations of insect numbers, defoliation amounts and tree-ring growth parameters to test the fidelity of the host-nonhost correction approach in reconstruction of past outbreaks to test the importance of climate variations on western spruce budworms and host trees.

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