



Periodicity of western spruce budworm in Southern British Columbia, Canada



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ABSTRACT

The western spruce budworm (WSB), *Choristoneura occidentalis* Freeman), a defoliator of conifers in western North America, causes severe timber losses to forests. In British Columbia, Canada, where the main species damaged is Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, outbreaks of *C. occidentalis* have been recorded since 1909. However, there is little information on the frequency of outbreaks of this defoliator for previous centuries. This information is needed to establish baselines defining the historic range of variability of this disturbance, to calculate potential depletions in timber supply from defoliation, and to refine forest management plans. Also, precise estimates of budworm recurrence are needed to assess potential ecosystem changes and possible departures from the historic range of this disturbance due to global warming. We used dendrochronology and time series analysis to determine past frequency of spruce budworm outbreaks in southern BC and found that, since the 1500s, outbreaks have been periodic, with a mean return interval of 28 years (95% Confidence Interval 21–35 years). No data was available before the 1500s. We found the number of outbreaks per century, since the 1800s, was fairly constant, with 3–4 outbreaks per century.

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1. Introduction

Spruce budworms, *Choristoneura* species (Lepidoptera: Tortricidae), are destructive defoliators of conifers in North America, causing tree mortality, growth loss and lumber defects. In terms of economic damage, the most important members of this genus are the spruce budworm, *Choristoneura fumiferana* Clem., a severe defoliator of the Canadian Boreal forest, and the western spruce budworm (WSB), *Choristoneura occidentalis* Freeman, a defoliator of conifers in western North America. Although *C. occidentalis* has been recently renamed *Choristoneura freemani* Razowski (Razowski, 2008), the new scientific name has not yet been adopted in North America. For this reason, in this paper we continue to use *C. occidentalis*.

In British Columbia (BC), Canada, where the main species damaged is Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, outbreaks of *C. occidentalis* have been recorded since 1909, with the earliest recorded outbreak occurring on south eastern Vancouver Island (Mathers, 1931; Harris et al., 1985), but records for this early outbreak are imprecise. More precise accounts of budworm outbreaks in BC started in the 1950s, when systematic ground surveys and increased use of aerial monitoring was initiated by the Forest In-

sect and Disease Survey (FIDS) of the Canadian Forest Service. However, with the exception of the work of Campbell et al. (2005, 2006), there is no published information on the frequency of outbreaks of this defoliator before the 1900s in BC. This information is needed to establish baselines defining the historic range of variability of this disturbance for use in forest management planning and to calculate potential depletions in timber supply from WSB outbreaks. Precise estimates of past budworm recurrence are also needed to assess potential ecosystem changes and possible departures from the historic range of this disturbance due to global warming.

The western spruce budworm lays its eggs on the underside of needles in July and August, shortly after the new adult moths have emerged from pupation and mated. Within 10–12 days eggs hatch and the new larvae overwinter without feeding, as second-instar larvae. Feeding begins after the larvae emerge from overwintering in mid to late May. Pollen cones, buds and old needles are mined until new foliage flushes and becomes available for feeding (Nealis, 2012). The larvae go through five instars before they pupate in late June to mid-July, and the one year cycle is completed 12–20 days later, when the new adults emerge (Furniss and Carolyn, 1977; Duncan, 2006). Outbreaks of *C. occidentalis* are economically important in BC; since 1990 and until 2011, defoliation has averaged over 500,000 ha per year (data provided by the Canadian Forest Service and the BC Ministry of Forests, Lands and Natural

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Resource Operations). The expected damage through growth loss and mortality is high enough to prompt the need for annual spray operations, in selected areas, aimed at protecting industry's timber supply (MacLauchlan and Buxton, 2012).

Douglas-fir occurs in a large area of south and central British Columbia identified as the Interior Douglas-fir (IDF) biogeoclimatic (BEC) zone (Krajina, 1965; Murdock et al., 2013). Other tree species susceptible to WSB defoliation in BC include Engelmann spruce, *Picea engelmannii* Parry ex Engelm., and subalpine fir, *Abies lasiocarpa* (Hook.) Nutt (Furniss and Carolyn, 1977).

The cross-section ring width sequence of trees record the variations in growth rates as influenced by the many factors affecting growth at the time of formation of the ring. The study of these variations forms the basis for the science of dendrochronology, which endeavors to reconstruct variation in conditions of growth over time (Speer, 2010). Periods of reduced growth are caused by adverse conditions such as drought or removal of foliage by insects. By removing foliage during the growing season, defoliating insects cause sequences of narrow rings in the years when foliage has been removed (Alfaro et al., 1982). Dendroentomology, a subfield of dendrochronology, documents past occurrence of forest insect outbreaks, and provides an understanding of insect population dynamics, including duration of outbreaks, interval between outbreaks and spread (Speer, 2010). The method relies on comparing the specific tree ring signal left by particular insect disturbance during outbreaks, to rings patterns in undamaged species in the same area. Dendroentomology has been used to explore the temporal periodicity and spatial variation of outbreaks of the two-year cycle budworm, *Choristoneura biennis* Freeman in BC (Zhang and Alfaro, 2002, 2003), the recurrence of western spruce budworm in BC (Campbell et al., 2005, 2006) and in the western United States (Swetnam and Lynch, 1989, 1993; Swetnam et al., 1995; Ryerson et al., 2003). Extensive dendroentomology work has also been completed to reconstruct the history of *C. fumiferana* in the boreal forest of eastern Canada (Blais, 1983; Boulanger et al., 2012; Jardon et al., 2003; Morin et al., 1993; Simard and Payette, 2001) and northern BC (Burleigh et al., 2002). These studies reveal periodicity in the population dynamics of the genus *Choristoneura* (Dutilleul et al., 2003; Jardon et al., 2003; Royama, 1984; Swetnam and Lynch, 1993).

The objective of this study was to use dendrochronology to reconstruct the history of WSB in the south central region of British Columbia and expand on the results of Campbell et al. (2005, 2006) by including additional areas in southern BC. The dendrochronological budworm history compiled by Campbell et al. (2005, 2006) was based on cores collected in a small area (about 15 by 15 km) at Opax Mountain near Kamloops, BC. Here we utilize the Campbell data, along with dendrochronology data from seven additional locations, to prepare a comprehensive history of budworm for Southern BC.

2. Methods

To identify past western spruce budworm outbreaks in southern British Columbia we compared annual growth patterns of trees affected by WSB (host trees) to growth patterns of non-host trees, utilizing the software program OUTBREAK (Holmes and Swetnam, 1996; Swetnam et al., 1995). This procedure removes the influence of factors that are not specific to WSB disturbance, such as ring width variations due to weather and that affect all tree species at a site. Remaining deviations are then assumed to be the result of species-specific activities of WSB (Swetnam and Lynch, 1993; Holmes and Swetnam, 1996; Ryerson et al., 2003). In this case, we used the sympatric species ponderosa pine (Py), (*Pinus ponderosa* Dougl., ex P. & C. Laws), as the non-host species, which has been

shown to share the same climate signal as Douglas-fir when growing in similar sites (Fritts, 1974).

2.1. Study area, data collection and chronology development

We obtained increment core data from eight locations in southern British Columbia (Table 1, Fig. 1). For analyses purposes, and based on proximity, these were grouped into five datasets: Railroad Creek, Stein Valley, Okanagan, Kamloops (two locations) and Cache Creek (three locations) (Table 1). All but one site is located in the IDF Biogeoclimatic zone of BC's hot and dry southern Interior Plateau, in subzones ranging from Xeric Hot to Wet Warm or Dry Cool (Meindinger and Pojar, 1991); the remaining site was in the Ponderosa Pine zone (Table 1), which is also xeric and hot. Elevation of sites ranged from 200 to 1310 m. Climate in these zones is characterized by a long growing season with dry summers and frequent moisture deficits (Lloyd et al., 1990).

The increment core data in this study come from different sources (Table 2). During the summer of 2012 the authors collected increment cores from the three Cache Creek sites and from the Railroad Creek site. One core per tree was collected at breast height from Douglas-fir trees, and from any locally available ponderosa pine trees, using a 5 mm Pressler increment borer. Sample sizes (number of trees cored per site) are given in Table 2. All cores were prepared in the lab following standard dendrochronology procedures as outlined by Stokes and Smiley (1996). Samples were scanned and measured using a WinDendro™ system (Regent Instruments Inc. 1995), with a measurement precision of 0.01 mm.

Archived tree ring data for Douglas fir and ponderosa pine for the area of interest was also used (Table 2). To be used in the study, archived data needed to be accurately cross dated, i.e., the dates assigned to each ring had been verified and had significant interserial correlation. Significant values of the interserial correlation of the tree ring series in a site indicate the presence of a strong common signal among the samples.

The Kamloops dataset was compiled from two existing sources: (1) Data from the Opax Mountain case study reported by Campbell et al. (2005, 2006), consisting of 630 Douglas-fir and 94 ponderosa pine cross-dated series, was made available to us by André Arsenaault, Canadian Forest Service, Cornerbrook, Newfoundland, and (2) the International Tree Ring Data Bank, ITRDB (<http://web.utk.edu/~grissino/itrdb.htm>), identified in Table 1 as Kamloops ITRDB. The Kamloops ITRDB dataset consisted of 22 Douglas-fir and 20 ponderosa pine cross-dated cores (Fritts, 2013a,b) (Table 2).

The Stein Valley data was also obtained from the ITRDB, and consisted of 15 Douglas-fir and 27 ponderosa pines, all cross-dated (Table 2) (Riccius et al., 2013a,b).

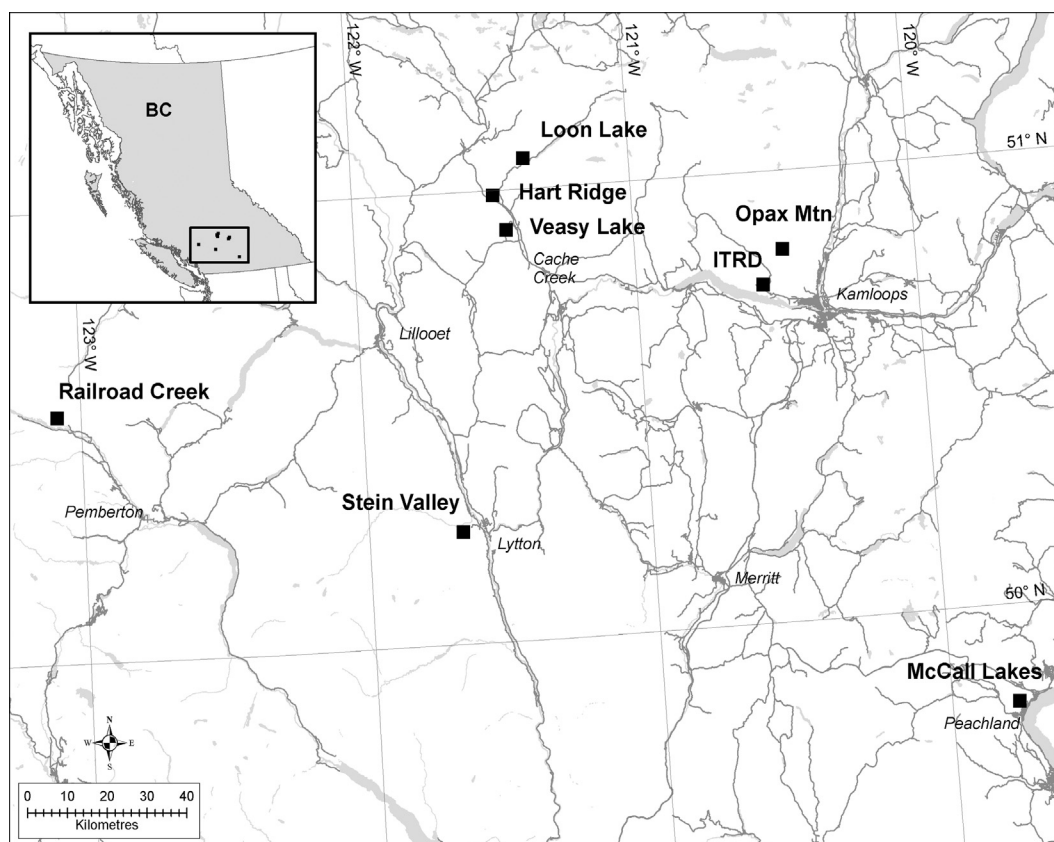
The Okanagan data set was derived from cores collected during the 2008 North American Dendroecological Fieldweek near Peachland, at McCall Lakes, by R. Alfaro and students attending the course (Alfaro et al., unpublished report, 2008). In this case, 64 Douglas-fir and 23 ponderosa pine cores were collected, cross-dated and archived at the Pacific Forestry Centre (Table 2).

Datasets obtained from these sources were reduced to one core per tree (when needed) by selecting the core with the highest interserial correlation, as reported by the authors of the datasets and eliminating, whenever possible, any trees less than 300 years old. The final sample size for each area and tree species is given in Table 2. These datasets were used to develop new Douglas-fir master chronologies for each of the five areas of interest (Table 2). Chronologies for each location were developed using the computer program COFECHA (Holmes, 1983) and standardized using the computer program ARSTAN (Cook and Krusic, 2005) using either a negative exponential curve, linear regression or a horizontal line as appropriate (Cook et al., 1990). Detailed descriptions of COFECHA and ARSTAN can be found in Speer (2010).

Table 1

Description of study sites in southern British Columbia, Canada, used to determine the periodicity of western spruce budworm outbreaks.

Location	Latitude	Longitude	Elevation (m)	BEC ^a	Subzone
1 Railroad Ck	50° 54' N	123° 08' W	557	IDF	Wet warm
2 Stein Valley	50° 15' N	121° 40' W	200	IDF	Dry cold
3 Okanagan	49° 47' N	119° 46' W	1030	IDF	Xeric hot
4 Kamloops					
Opax Mtn	50° 49' N	120° 28' W	1310	IDF	Dry cool
ITRDB	50° 45' N	120° 33' W	822	PP	Xeric hot
5 Cache Creek					
Hart Ridge	50° 54' N	121° 27' W	982	IDF	Xeric hot
Loon Lake	50° 59' N	121° 22' W	958	IDF	Xeric warm & dry cool
Veasy Lake	51° 04' N	121° 22' W	811	IDF	Xeric hot

^a BEC = Biogeoclimatic zone of British Columbia.**Fig. 1.** Locations used to study the periodicity of western spruce budworms in southern British Columbia.**Table 2**

Dendrochronology summary statistics for Douglas-fir and ponderosa pine from southern British Columbia used to determine historic western spruce budworm outbreaks.

Chronology	Chronology period (AD)	No. of cores	No. of years	Interserial correlation	Mean sensitivity	Year at 5 tree minimum
<i>Douglas-fir chronologies</i>						
Railroad Creek	1673–2011	23	339	0.532	0.190	1699
Stein Valley	1598–1995	11	398	0.548	0.216	1790
Okanagan	1619–2008	43	390	0.644	0.273	1803
Kamloops	1505–2000	26	496	0.582	0.333	1600
Cache Creek	1623–2012	30	390	0.683	0.358	1753
<i>Ponderosa pine</i> ^a						
Stein Valley	1496–1995 ^b	12	499	0.380	0.299	–
Okanagan	1810–2007 ^b	12	197	0.446	0.446	–
Kamloops, ITRDB	1576–1965 ^b	6	389	0.575	0.367	–
Kamloops, Opax	1763–2000 ^b	9	237	0.538	0.538	–
Cache Creek	1685–2011 ^b	11	326	0.417	0.298	–
Regional Master	1496–2011 ^b	50	516	0.531	0.301	1613–2007

^a No individual site chronologies developed.^b Dates are given for the range in individual trees at each site.

2.2. Non-host chronology

Because of scarcity of old ponderosa pine trees due to a mountain pine beetle infestation that begun in the area about 10 years earlier, sample size per location for the non-host species was low (Table 2). Therefore, we decided to prepare a regional non-host master chronology by combining ponderosa pine core data from all areas where ponderosa pine was collected (Cache Creek, Kamloops, Okanagan, and Stein Valley, Table 2). No ponderosa pine was available at the Railroad Creek site. This chronology was based on 50 cores and had significant interserial correlation ($r = 0.531$, $P < 0.01$). We considered this chronology robust for the period represented by a minimum of five sample trees, which commenced in the year 1613.

2.3. Outbreak reconstruction

The program OUTBREAK was used to identify WSB outbreaks in each of the five study areas (Holmes and Swetnam, 1996). The regional climate signal was removed from the data by correcting individual host tree series with the regional non-host ponderosa pine master chronology.

WSB outbreak detection was based on patterns of growth reduction in tree rings that are known to be associated with WSB defoliation: growth reduction due to defoliation usually lasts for at least 8 years, with ring widths remaining at a level below 1.28 standard deviations relative to the mean series for this period. These factors are adopted from empirical studies by Alfaro et al. (1982), Campbell et al. (2006), Ryerson et al. (2003). Using the minimum outbreak duration of 8 years in OUTBREAK reduces the possibility of confounding the pattern of reduced rings caused by WSB with that of reduced rings caused by defoliation by the Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough), a common defoliator of Douglas-fir occurring in the same area. Outbreaks of the Douglas-fir tussock are much shorter than those of WSB, lasting only 3–5 years (Alfaro et al., 1987; Speer, 2010).

Runs of this program produce an outbreak chronology, which contains the annual percentage of trees that meet the WSB growth reduction signal outlined above. For a given location, years of growth reduction were assumed to be due to budworm outbreak when 20% or more of the trees in that location exhibited the specified growth reduction signal. The percentage of trees in a stand showing WSB growth suppression is a proxy measure of outbreak intensity. During light defoliation years many trees escape defoliation and show no suppression on tree rings. On the contrary, nearly all trees in the stand sustain growth suppression during severe defoliation episodes (Alfaro et al., 1982).

It must be noted that for dating outbreaks, the growth reduction signal caused by budworm generally consists of two phases (Alfaro et al., 1982). The first phase occurs during the period of active larval feeding, during which ring widths decline to a minimum. The second, a recovery phase, follows the collapse of the outbreak, during which rings become progressively wider as defoliated trees regain a full crown. Each phase is approximately one half of the total length of the growth reduction period. Therefore, when dating budworm events, we report a year as an outbreak year only if it occurs during the active feeding phase of declining rings.

In addition to each of the five individual outbreak reconstructions we developed a regional reconstruction of WSB outbreaks for the study area by summing the number of trees expressing the annual WSB growth reduction signal in OUTBREAK from all five areas and expressing it as a percentage of the total number of sample trees in all locations (Ryerson et al., 2003; Campbell et al., 2006). The regional reconstruction was used to prepare a single composite history of budworm activity back in time into the 1600 and 1700s, as well as to determine outbreak periodicity. A

single individual Douglas-fir tree, dating back to 1505, was also corrected with the Outbreak program to determine any possible budworm activity in the 1500s.

Outbreak recurrence in each of the five areas and in the regional chronology was investigated using the following two approaches:

- (1) Interval Method. We calculated WSB return intervals for each of the five areas as the number of years between outbreak start dates in the outbreak chronology. Mean return intervals and standard deviation were calculated for each location and for the regional master outbreak chronology.
- (2) MTM Method. We applied the multi-taper method (MTM) of spectral analysis to each of the five outbreak chronologies (Thompson, 1982; Mann and Lees, 1996). For this we used the Singular Spectrum Analysis - MultiTaper Method (SSA-MTM) Toolkit, a software program to analyze noisy time series. A description of this program, and its theoretical basis can be found in http://www.atmos.ucla.edu/tcd/ssa/#ssa_ssa (accessed November 28, 2013). We reported detected periodicities with confidence level set at 99%.

In addition, we tested for potential changes in outbreak frequency during the 1800s and 1900s (the period covered by all five chronologies) using a chi-square test (Mendenhall, 1975) based on the number of outbreaks per century at each of the five sites.

3. Results

Douglas-fir chronologies were well cross-dated in all five locations, with significant interserial correlation above 0.53 at each location ($P \leq 0.01\%$) (Table 2). The Kamloops Douglas-fir chronology was the longest host chronology and was considered robust (having a replication of at least 5 trees) from the year 1600 onward. The individual ponderosa pine chronologies also had significant interserial correlation, ranging from 0.380 to 0.575 (Table 2); the regional master ponderosa pine chronology had a significant interserial correlation of 0.531 and was robust for the period between 1613 and 2007.

3.1. Outbreaks in the 1800s and 1900s

All five sites shared a common chronology interval starting in the 1800s and lasting until the late 1900s, and showed recurrent spruce budworm outbreaks (Fig. 2). In the regional chronology (Fig. 3) we identified four region-wide outbreak episodes during the 1800s (~1800s–1820s, 1850s–60s, 1870s–1880s, and 1890s–1900s) and three outbreaks for the 1900s (1930s–1940s, 1970s–1980s, 1980s–1990s).

The first outbreak of the 1800s (~1800 to 1820) was synchronous across all locations and was the most prominent, both in duration and severity (as determined by the percentage of trees in the sample that showed an outbreak signal) (Figs. 2 and 3). The growth reduction signal for this outbreak lasted approximately 40 years; therefore, we inferred an active feeding phase of approximately two decades (1/2 of the growth suppression period). This outbreak also recorded the highest percentage of trees sustaining growth reduction relative to the other outbreaks, ranging from 77% to 100%, depending on location (Fig. 2). Another prominent outbreak began in the early 1930s and lasted until the early 1940s, with a high percentage of trees recording growth reductions ranging from 58% to 84%. The average duration for this outbreak was shorter than the 1800s outbreak, but at 10 years, it is within the expected range of duration for WSB.

A comparison of the number of growth reduction periods attributable to budworm (outbreak frequency) in the 1800s and 1900s

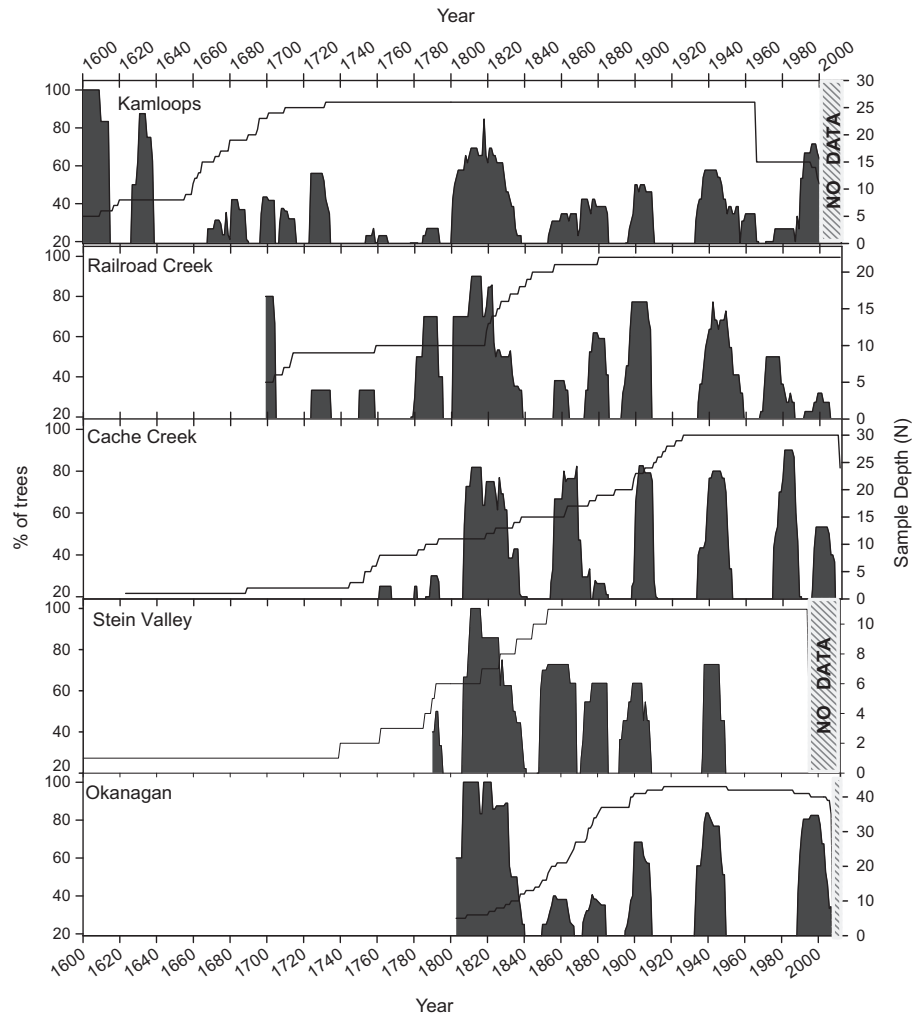


Fig. 2. Percent of trees recording WSB outbreaks (shaded area) through time, in five areas of southern British Columbia. Left axis scale is truncated to the 20% of the trees showing the growth reduction signal of WSB in outbreak. Solid line indicates the sample depth as number of trees at each location.

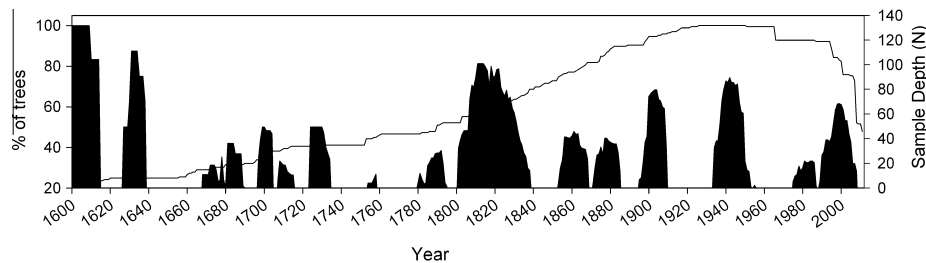


Fig. 3. Regional outbreak chronology of percentage of trees recording western spruce budworm outbreaks through time. Left axis scale is truncated to the 20% of the trees showing the growth reduction signal of WSB in outbreak. Solid line indicates the sample depth as number of trees at each location.

indicated no significant differences between these two centuries, which each had three or four outbreaks per century (Chi square test, $p > 0.933$, $df = 4$, $N = 5$) indicating that the return interval for WSB has remained constant for at least 200 years.

3.2. Comparison of budworm history based on tree rings with historic survey data

Overall, our reconstructions agree with the written accounts of WSB outbreaks in southern B.C. for the 20th century (no records exist before that). However, these comparisons need to take into consideration the fact that systematic aerial surveys in BC begun

only in the 1950s; we have only partial written accounts for the first half of the 20th century (summarized by Harris et al., 1985). The earliest written account of WSB activity within our study area was a report of an infestation in 1916 in the Lillooet area of BC (Harris et al., 1985). Our chronologies suggest that this report refers to the tail end of a large WSB outbreak that affected Southern BC, which started in the late 1800s and extended into the 1900s (Fig. 2). This outbreak was widespread and synchronous, as it was detected in all five locations in our study (Fig. 2).

The widespread and spatially synchronous outbreaks detected in our reconstructions during the late 1940s in all five locations (Fig. 2) correspond with written accounts for British Columbia for

three of the five areas in this report (Harris et al., 1985): Railroad Creek, Cache Creek and Stein Valley. However, Harris et al. (1985) do not mention outbreaks in this period for the Okanagan, or Kamloops sites. We attribute the discrepancy to inaccurate budworm mapping in these early survey years.

Our reconstructions correspond well with the published record for the remaining two outbreaks of the 20th century in our areas (which by then were based on systematic aerial surveys), the 1970–1980s and 1989–1999 outbreaks, both in terms of presence and absence of budworm signal in the tree ring record in a given location. The cartographic history of the WSB for the period starting in the 1970s has been described in detail (Harris et al., 1985; MacLauchlan et al., 2006) and indicates severe outbreaks starting in the 1970s in the Fraser Canyon and Railroad Creek area of BC, collapsing there in 1977. However, following the end of this infestation, additional outbreaks developed north and east, into the Cache Creek, Kamloops and Okanagan areas in the 1980s. This lack of spatial synchronicity and the temporal-spatial dynamics of this outbreak are evident in our tree ring reconstructions. For example, the Stein Valley (near the Fraser Canyon) and Okanagan chronologies show no evidence of the 1970–1980s outbreak (Fig. 2). This coincides with the precise survey data reported by Harris et al. (1985), which indicates that the Stein Valley location sustained only one year of light defoliation (1977) during the large Fraser Canyon outbreak (Harris et al., 1985). The Okanagan Lake area was affected only starting in the late 1980s after the collapse of the 1970s outbreak in the Fraser Canyon of BC (Erickson, 1987).

3.3. Older outbreaks

The regional chronology suggests four budworm episodes during the 1700s, with the first in the early 1700s (a continuation of an outbreak that began in the late 1690s), followed by outbreaks

in the mid-1720s, early 1750s, and 1780s (Fig. 3). However, this portion of the regional chronology is represented by data from only the Railroad Creek and Kamloops sites (Fig. 2), and consequently we are unable to comment on the geographic extent of these outbreaks.

The long Kamloops chronology indicated four WSB outbreaks in this area during the 1600s (Fig. 2) (~1600–1607, mid-1620s to mid-1630s, late 1660s to ~1680, and late 1690s).

A tree ring series derived from a single Douglas-fir tree, dating to the early 1500s and corrected by the regional Py chronology, suggests that there may have also been a WSB outbreak in the 1520s and again in the 1540s–50s at the Kamloops site (Fig. 4). However, confirmation of these outbreaks requires additional sampling.

3.4. Budworm periodicity in southern BC

Based on the interval method of determining outbreak recurrence, the mean WSB return interval across all five locations, and for the last 200 years (1800 and 1900s) was 30 years, varying from 26 in Cache Creek to 37 years in the Okanagan (Table 3). However the standard deviation of the return interval for individual locations averaged 13 years, indicating that the return intervals for these five locations were not significantly different. The return intervals for WSB in northeast Oregon and the southern Rocky mountains showed a wider range than our studies, from 21 to 53 years and 14 to 58 years, respectively (Swetnam et al., 1995; Swetnam and Lynch, 1993).

The multi-taper method (MTM) indicated significant oscillatory modes at all five locations and provided WSB return periods which were comparable to those obtained by the interval method (Table 3). Three of the five locations (Kamloops, Railroad Creek and Okanagan) indicated 30–34 year cycles at the 99% confidence level;

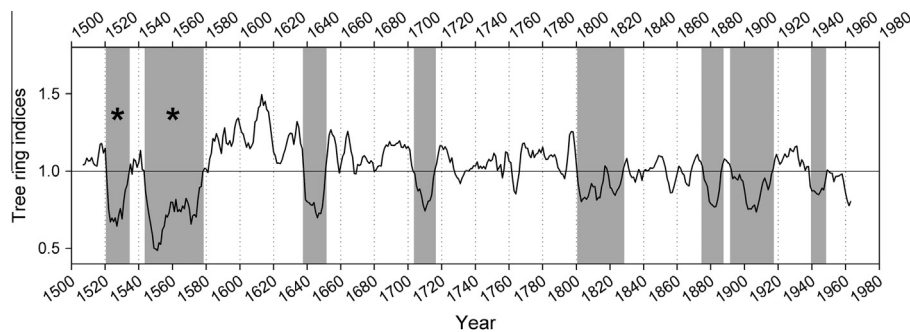


Fig. 4. Tree ring indices for the oldest Douglas fir tree (1505–1965) corrected by the non-host master chronology using the Outbreak program. Shaded areas indicate periods of significant growth reduction indicative of budworm outbreaks. *Indicate periods of growth reduction attributed to budworm for dates before the outbreak chronology for the area.

Table 3

Length, total number of western spruce budworm outbreaks in chronology, mean outbreak duration (1/2 of growth reduction period, see text), outbreak return interval and significant oscillatory modes in five locations in British Columbia, Canada.

Location	Outbreak chronology		Outbreak duration (years)		Return interval (years)		Multi-taper method (MTM) ^a		
	Length (years)	No. outbreaks	Mean	SD	Mean	SD	Significant Oscillatory Modes		
Railroad Creek	252	11	8	±5	29	±11	21		
Stein Valley	206	6	9	±5	30	±13	19		
Okanagan	205	6	11	±5	37	±15	34		
Kamloops	400	15	8	±5	27	±13	30	5	3
Cache Creek	258	10	7	±5	26	±13	34	21	
Mean			9		30	±13			
Regional	400	15	7	±4	28	±12	33	24	19

^a Significance level at >= 99% c.

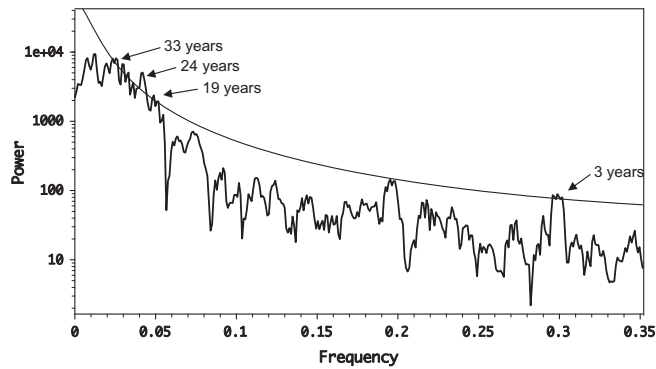


Fig. 5. Multi-taper analysis results of the regional outbreak chronology for western spruce budworm in southern British Columbia. The steadily declining line shows the 99% significant level for the oscillatory modes.

also, there was a 19–21 year oscillation in three of five locations (Railroad Creek, Cache Creek and Stein Valley). Cache Creek was the only site that had both 34 and 21 year cycles (Table 3). Previous time series analysis for WSB in the Kamloops area found significant periodicities at 30, 43, and 70 years (Campbell et al., 2006), while in Colorado, the WSB had significant periodicities at 25, 37, and 83 years (Ryerson et al., 2003). Our results did not indicate any significant oscillatory modes in the upper range of 70–83 years. Instead, secondary, much shorter oscillatory modes, between 3 and 5 years, were also present in one of the five locations (Kamloops chronology) (Table 3). Comparing these results with those obtained with the interval method we noted that the first two oscillatory modes of 19–34 years are within the 95% confidence limits of the interval method, which led us to conclude that, based on the MTM method, the mean WSB return interval for southern BC, ranges from 19 to 34 years (Table 3).

When applied to the regional outbreak chronology, both interval and MTM methods provide similar estimates of outbreak periodicities relative to the individual locations: 28 years (standard deviation of 12 years, 95% Confidence Interval of 21–35 years) for the interval method and 19–33 years for the MTM method (Fig. 5).

4. Discussion

Historic records overlap our study area from 1916 to 2012 with three regional outbreak episodes reported for this period. Our tree ring study shows good concordance between the tree ring record and the historic reports for this period, with all three outbreaks in this period visible in the tree ring record. At the regional scale our analysis identified fifteen WSB outbreaks over the past 400 years in southern British Columbia.

Some of the budworm literature from the US has suggested increasing budworm activity in the 20th century as a result of human activities, e.g., tree harvesting and fire suppression, possibly altering forest characteristics, which would increase their susceptibility to budworm outbreaks (Swetnam and Lynch, 1993; Swetnam et al., 1995). However, our study did not support this hypothesis. Our results indicated no change in outbreak frequency between the 19th and 20th century, with 3 to 4 outbreaks per 100 years. This result coincides with those of Ryerson et al., (2003) in the US northwest and Royama (1984) for *C. fumiferana* in eastern Canada. Royama (1984) reports an outbreak frequency of 3 outbreaks per 100 years for both New Brunswick and Quebec. One possible explanation for the difference between our findings of stable outbreak frequency and the studies of Swetnam and Lynch (1993) and Swetnam et al. (1995) may be a scale issue: we only sampled

eight sites in five locations, and regional variability was evident in the much larger US studies.

The reconstruction of western spruce budworm outbreaks for southern British Columbia reported in this paper demonstrates the cyclical nature of the population dynamics for this insect in BC, confirming the existing literature with respect to the periodic nature of the genus *Choristoneura* (Dutilleul et al., 2003; Swetnam and Lynch, 1993; Royama, 1984). The primary oscillatory modes represented in our outbreak chronologies of 19–33 years are well within the range of other spruce budworm studies. Swetnam and Lynch (1993) reported cycles of ~20 to 33 years in northern New Mexico, and Royama (1984) working with *C. fumiferana*, reported average cycle length of 35 years for in New Brunswick and 38 years for Quebec.

In his exhaustive analysis and modeling of the population dynamics of *C. fumiferana* in New Brunswick, Royama (1984) concluded that the observed periodic spruce budworm cycles were caused by density dependent mortality factors specific to the dynamics of budworm, particularly budworm parasitoids and disease. He concluded that other mortality factors, such as predation, food supply shortages, weather and dispersal losses were not as important causes of population cycles.

MTM analysis on the regional chronology also indicated a short secondary oscillation every 3–5 years (Table 3, Fig. 5). We hypothesize that this short oscillatory mode could be caused by an endogenous rhythm in the tree populations, such as mast (seed) years. El-Kassaby and Barclay (1991) demonstrated that Douglas-fir produces narrow rings during mast years. However, this short cycle is apparent only in the Kamloops series.

Synchronous outbreak activity was evident at a regional scale in our study; however, we did observe localized variations in WSB outbreak synchrony (absence of the 1970s outbreak in two locations). These variations could be due to localized differences in stand characteristics that render particular sample stands less susceptible to budworm. However, these variations did not obscure a general trend towards synchronous outbreaks. Two primary explanations for spatial synchronization of separate insect populations have been proposed: dispersal and the Moran effect (Moran, 1953; Royama, 1984). Proponents of synchronization through dispersal (Berryman, 1987) indicate that population expansion and dispersal may lead to synchronized outbreak waves. Alternatively, the literature suggests that over large areas, exogenous cues, such as climate, maybe responsible for synchronizing insect outbreaks regardless of the density dependent mechanisms at play (Royama, 1984; Myers, 1998; Williams and Liebhold, 2000; Koeing, 2002; Jardon et al., 2003). Gypsy moth, *Lymantria dispar* (L.), for example has been shown to be operating in synchronicity up to distances of 1200 km within continents (Johnson et al., 2005), however, other studies of gypsy moth in North America have shown synchronous behavior to wane with distances greater than 600 km (Peltonen et al., 2002). In our case, WSB was synchronous in our entire study area, which encompassed an area ~247 km from East to West and ~136 km from North to South.

Understanding historic periodicity and spatial synchrony of outbreaks is important for establishing baselines of ecosystem function and the historic range of variation of budworm disturbance. This study will help resource managers who need to include budworm as a depletion agent in forest management planning and future timber supply calculations.

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