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Multicentury reconstruction of western spruce budworm outbreaks in central British Columbia, Canada

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ABSTRACT

The western spruce budworm (*Choristoneura occidentalis* Freeman; WSB) is a widespread and destructive defoliator of commercially important coniferous forests in western North America. In British Columbia, Canada, Douglas-fir (*Pseudotsuga menziesii*) is the most prevalent host, and records show that significant outbreaks have primarily occurred in the southern interior over the last century. In the central interior of British Columbia, particularly in the Cariboo Forest Region, the most recent outbreak of western spruce budworm, which is in its second decade, has been severe and widespread. It is perhaps due to this long outbreak, which is unprecedented in duration since detailed surveys began in the 1950s, that there is an anecdotal perception that the western spruce budworm is expanding its range northward into the region, affecting Douglas-fir near the edge of its northern distribution. However, very little is known about the long-term outbreak history of western spruce budworm in the central interior of the province. In this study we used 11 Douglas-fir host chronologies and 2 regional *Pinus* non-host chronologies to reconstruct western spruce budworm outbreaks over a 435-year period. Standard dendrochronological techniques were used to develop tree-ring chronologies at each site and the program OUTBREAK was used to detect outbreak periods. We reconstructed 12 outbreaks starting in early 1600s with a mean return interval of 30 years. Sensitivity analysis illustrated that including light, moderate and severe intensity thresholds modified the number of reconstructed outbreaks, their duration and mean return interval. Sub-regional chronologies based on biogeoclimatic subzones and variants (BEC units), revealed strong synchrony of some outbreak events, but not all. Wavelet analysis of the sub-regional chronologies demonstrated the quasi-periodic behavior of western spruce budworm over the entire record, which averaged 32-years. By reconstructing WSB dynamics over 400 years we demonstrated that outbreaks observed over the last 40 years in the Cariboo Forest Region are not unprecedented.
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1. Introduction

Budworms in the genus *Choristoneura* (Lepidoptera: Tortricidae) that feed on conifers periodically experience population outbreaks that extend over large geographical areas in North America. Notable in this regard is the western spruce budworm (WSB; *Choristoneura occidentalis* Freeman), a widespread and destructive defoliator in western North America (Fellin and Dewey, 1982) that primarily feeds on Douglas-fir (*Pseudotsuga menziesii* var. *glauca* Beissn. Franco), but also on true firs (*Abies* spp.), Engelmann spruce (*Picea engelmanni* Parry ex Engelm.) and western larch (*Larix occidentalis* Nutt.) (Furniss and Carolin, 1977; Fellin and Dewey, 1982). Repeated and/or sustained WSB outbreaks can result in large timber volume losses, stem defects, mortality primarily in understory trees, and regeneration delays due to budworm feeding on developing cones (Alfaro et al., 1982; Fellin and Dewey, 1982; van Sickle et al., 1983; Alfaro and Maclauchlan, 1992; Hadley and Veblen, 1993; Maclauchlan and Brooks, 2009).

Since the early-1900s documented WSB outbreaks in the Douglas-fir forests of British Columbia (BC) has resulted in the defoliation of over 5.6 million hectares (Maclauchlan et al., 2006). Despite the fact that Douglas-fir is one of the most commercially valuable conifer species in BC, attention to WSB outbreak dynamics has primarily been confined to the southern interior of the province (Harris et al., 1985; Maclauchlan et al., 2006) where tree-ring studies show that over the last 500 years WSB outbreaks have occurred repeatedly, with a mean return interval of approximately

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33 years (Campbell et al., 2006; Alfaro et al., 2014). Typically these outbreaks are demarcated in annual tree rings by periods of reduced incremental growth that last through the outbreak and a number of years following outbreak cessation (i.e., recovery period) (Alfaro et al., 1982).

Little is known about the long-term WSB disturbance history in the Cariboo Forest Region of central interior BC. Systematic Forest Insect and Disease Surveys (FIDS), which began in the early 1950s, first documented WSB outbreaks in 1974 (Erikson, 1992), and by the late-1990s over 200,000 hectares were experiencing moderate to severe defoliation (Westfall and Ebata, 2000–2011). Since that time, WSB defoliation has occurred episodically across the BC interior and in 2003 increased to encompass >500,000 hectares (Maclauchlan et al., 2006). Overlay analyses in the Thompson–Okanagan Forest Region, immediately south of the Cariboo Forest Region, suggests that defoliation since the 1980s is historically unprecedented in duration and extent (Maclauchlan et al., 2006).

The recent history of defoliation in the Thompson-Okanagan Forest Region suggests that WSB may be expanding its range northward into the Douglas-fir forests of the adjoining Cariboo Forest Region in response to ongoing climate change (Murdock et al., 2012). Given that WSB defoliation in this region would result in significant depletions in the assumed timber supply (BCMFR, 2007; Woods et al., 2010), developing a comprehensive understanding of long-term forest-budworm interactions is essential for updating current forest management strategies (Shepherd, 1994; BCMFR, 1995).

The purpose of this study was to develop multi-century reconstructions of WSB outbreaks in the Cariboo Forest Region using dendrochronological techniques. Specifically, we sought to determine the historical frequency of WSB outbreaks; the degree of regional outbreak synchrony; and the periodicity of outbreaks across multiple centuries. Dendrochronology has been previously used in southern BC and in the western United States (US) to reconstruct WSB outbreak histories, as well as to provide temporal and spatial insights on outbreak dynamics across multiple centuries (Swetnam and Lynch, 1989, 1993; Ryerson et al., 2003; Campbell et al., 2005, 2006; Alfaro et al., 2014; Flower et al., 2014). These studies have demonstrated the periodic nature of outbreaks (Hadley and Veblen, 1993; Alfaro et al., 2014), their spatial synchrony across scales (Swetnam and Lynch, 1989; Hadley and Veblen, 1993; Campbell et al., 2006), and offer insights as to how forest management activities influence outbreak dynamics (Maclauchlan and Brooks, 2009).

2. Methods

Historical WSB outbreaks are identified by detecting periods of sustained growth suppression in Douglas-fir tree-ring records (Swetnam and Lynch, 1989; Alfaro et al., 1982). Feeding by WSB on current year buds and foliage reduces or eliminates apical growth during each year of defoliation. After an outbreak collapses the surviving trees then take several years to regain full foliage and for the annual growth ring to return to pre-outbreak increments (Alfaro and Maclauchlan, 1992). To detect the duration and frequency of WSB outbreaks dendrochronological studies commonly remove the climate-driven component of radial growth contributing to inter-annual variation. This variation is 'corrected' using a chronology from a non-host tree species, i.e., a tree species that is not defoliated by the budworm, but is sensitive to the same climatic conditions as the host. Periods of sustained growth reduction remaining in the corrected host chronology are inferred to result from WSB defoliation (Swetnam and Lynch, 1989).

2.1. Study Area

The Cariboo Forest Region extends from 51°00′ to 52°30′ north latitude and from 120°30′ to 125°45′ west longitude in the BC central interior (Fig. 1). The Fraser Plateau makes up a large portion of the region and is characterized by a level to gently rolling landscape incised by river valleys, and local uplands with elevations predominantly ranging from 900 to 1500 metres above sea level (masl). The Chilcotin Plateau extends along the western periphery of the region, beyond which the Coast Mountains rise sharply to elevations up to 4000 masl. This landscape configuration results in a strong rain shadow effect and the western Chilcotin is the driest portion of the study area, with average annual precipitation at Tatla Lake averaging 403 mm/yr. As Pacific air masses move further eastward towards Williams Lake, humidity levels and precipitation increase slightly, with annual precipitation totals averaging 417 mm/yr (Wang et al., 2012). Summer months are typically dry, with most precipitation resulting from numerous convective storms. In the winter months Arctic air masses result in extended periods of extreme cold temperatures (Steen and Coupé, 1997).

In BC the biogeoclimatic ecosystem classification (BEC) uses vegetation, soils, and topography to identify geographic areas, referred to as biogeoclimatic zones, which have a relatively uniform climate. BEC zones are further divided into subzones based on the moisture and temperature regime of the area, respectively and some BEC subzones are further classified into variants based on their location or distribution within a subzone (Meidinger and Pojar, 1991). In the Cariboo Forest Region, the Interior Douglas-fir (IDF) BEC zone makes up approximately 45% (17,000 km^2) of the area and is located above the valleys of the Fraser, Chilcotin, and Chilanko rivers (Steen and Coupé, 1997). The very dry-warm (xw) and very dry-mild (xm) subzones are the driest and warmest in the region, and are transitional between grassland and forest (Table 2). The dry-cool (dk) subzone covers the largest area in the Cariboo Forest Region and is comprised of four variants, with the Chilcotin variant (dk4) being the coldest and driest (Steen and Coupé, 1997; Table 2). Herein, we shall refer to BEC subzones (e.g., xm) and BEC variants (e.g., dk4) simply as BEC units.

Tree species characterizing the Cariboo Forest Region include Douglas-fir, lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) and at low elevations in the southern portion of the region, ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws). In a study of Douglas-fir growth in BC, Chen et al. (2010) found that radial growth trends across all interior regions was positively correlated with precipitation in the fall of the previous year and in the current growing season, while radial growth was negatively correlated with temperature of the current growing season, suggesting that water stress is an important parameter limiting radial growth. Griesbauer and Green (2010) found that Douglas-fir radial growth was strongly correlated with previous July to current June precipitation, with moisture sensitivity most pronounced at the dry southern margins of the region. The radial growth of ponderosa pine is correlated positively to previous August and current July precipitation (Watson and Luckman, 2002), and negatively to current June temperature (Campbell et al., 2006), while radial growth of lodgepole pine is correlated positively to previous July and current June–July precipitation (Watson and Luckman, 2002; Lo et al., 2010; McLane et al., 2011).

The negative radial growth correlations exhibited by all three tree species to summer temperature in interior BC suggests that increased evaporative losses and water stress during high temperature intervals are detrimental to tree growth (Watson and Luckman, 2002). In mid- to low elevation interior ecosystems, tree-ring variability is primarily related to factors affecting water supply, especially precipitation, indicating that tree growth is lim-

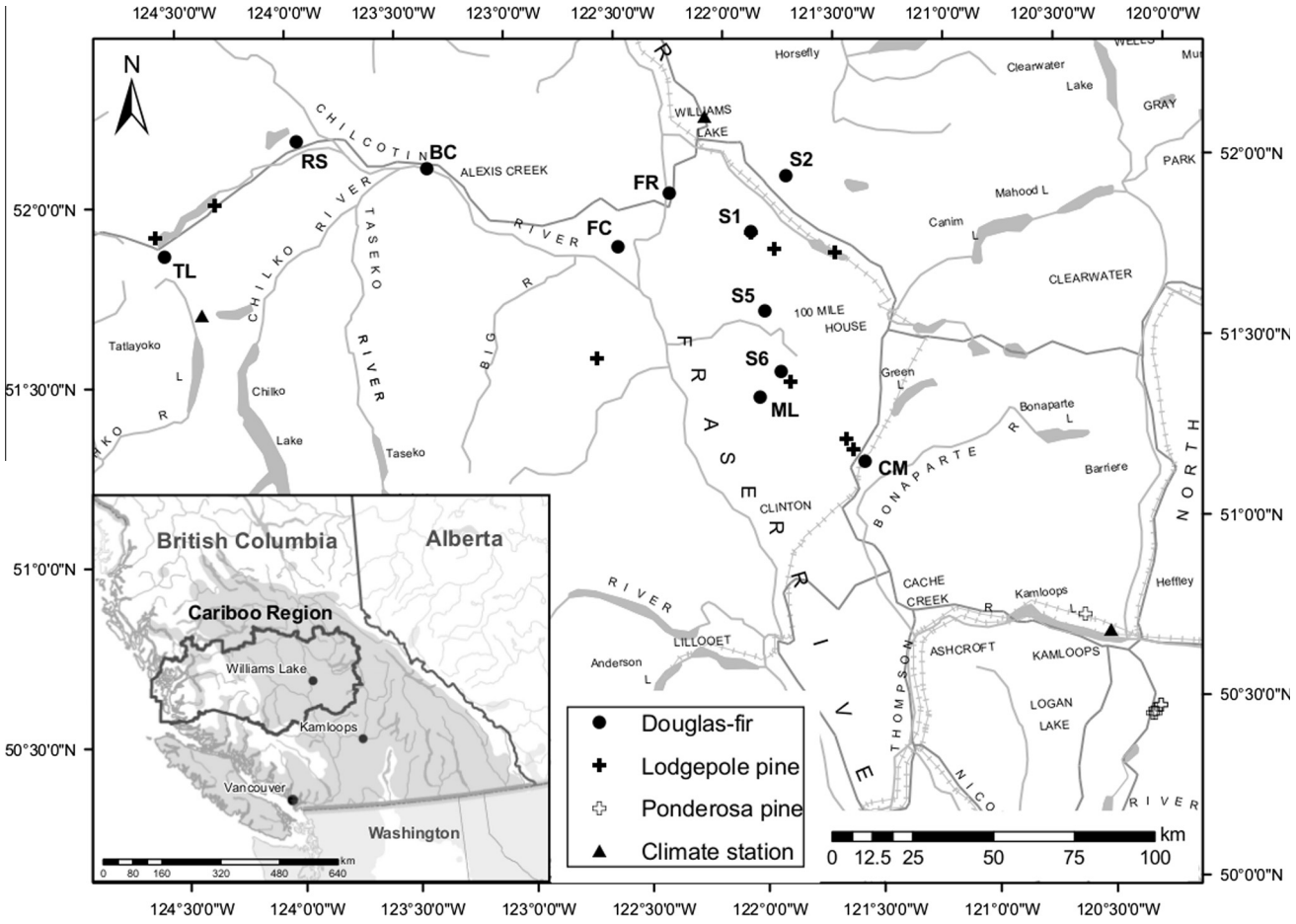

Fig. 1. Location of western spruce budworm host (Douglas-fir) and non-host (pine species) tree ring chronologies and climate stations in the Cariboo Forest Region, British Columbia, Canada (see Table 1 for chronology abbreviations). Inset map shows the outline of the Cariboo Region and the range of Douglas-fir in grey shading (Little, 1971).

ited by moisture availability in the previous and current growing seasons (Watson and Luckman, 2002; Campbell et al., 2006; Littell et al., 2008; Chen et al., 2010; Griesbauer and Green, 2010; Lo et al., 2010; McLane et al., 2011).

2.2. Sample collection, preparation and outbreak detection

One difficulty in reconstructing WSB outbreaks in the Cariboo Forest Region is the limited availability of long-lived non-host *Pinus* trees. The recent mountain pine beetle outbreak affected 18.1 million hectares of mature forest in BC (BCMFLNRO, 2012), decimating *Pinus* species across their geographic distribution. As a consequence, it was necessary to access previously collected tree-ring data to construct non-host chronologies for our study. Lodgepole pine chronologies were archived at the Pacific Forestry Centre (Alfaro et al., 2004) and at the University of British Columbia Tree-Ring Laboratory (Daniels and Watson, 2003). Ponderosa pine chronologies were archived at the International Tree-Ring Data Bank (ITRDB), the University of British Columbia Tree-Ring Laboratory (Daniels and Watson, 2003), and at the University of Victoria Tree-Ring Laboratory (Campbell et al., 2005, 2006). While the convention in tree-ring based reconstructions of WSB is to collect host and non-host chronologies from the same or adjacent forest stands (e.g., Swetnam and Lynch, 1989), as has been the case in other studies (Boulanger et al., 2012; Alfaro et al., 2014) we chose to combine the individual site data into species-specific regional non-host chronologies. Despite the large spatial extent of the study area previous work has demonstrated the strong moisture response of both pine species, and by constructing regional non-host chronologies any non-climatic growth responses were minimized while the regional climatic patterns were enhanced (Ryerson et al., 2003).

All host (Douglas-fir) and non-host (lodgepole pine and ponderosa pine) chronologies were developed by preferentially sampling trees at breast height with 5.2 mm diameter increment borers, collecting two cores from a minimum of 20 trees. After air drying, the cores were glued to slotted mounting boards and sanded to a fine polish (180–600 grit sandpaper) until individual tracheids within the annual rings were visible under the microscope. Tree ring-widths were measured using either WinDENDRO (2009b, Regents Inc. 2009) or a Velmex uniSlide digitally encoded traversing table at a precision of 0.01 mm. The measured ring-width series from individual sites were visually cross-dated and the list method was used to identify possible errors in measurement due to false or locally absent rings (Yamaguchi, 1991). Cross-dating was verified using the program COFECHA (Holmes, 1986). Douglas-fir sites developed at locations less than 10 km apart were combined into a single chronology. Individual ponderosa and lodgepole pine sites were cross-dated and then combined into species-specific regional non-host chronologies (Fig. 1, Table 1). Tree-ring series were standardized to remove the biological and geometric growth trends using the program ARSTAN (Cook et al., 2007). In ARSTAN, user-defined curves were applied to each measurement series and a bi-weight robust mean was computed using a mean value function that minimized the effect of outliers, producing a dimensionless stationary index time series with a defined mean of 1.0 and a

Table 1
Properties of western spruce budworm host and non-host chronologies in the Cariboo Forest Region of British Columbia, Canada. Chronologies are arranged from east to west (Fraser River to Tatlayoko Lake) and from the north to south (Farwell Canyon to Chasm, see Fig. 1) of the study area.

Site name	Site ID	Latitude	Longitude	Elevation (masl)	Source[a]	BEC units[b]	Series length	No. dated series	Inter-series *r*	AC[c]
Host-Douglas-fir										
Fraser River	FR	51°59′34″	122°17′11″	670	2010–11	IDFxm	1585–2010	57	0.73	0.66
Bull Canyon	BC	52°05′20″	123°21′53″	760	2010–11	IDFxm-dk4	1560–2009	38	0.75	0.49
Redstone	RS	52°09′35″	123°54′08″	990	2010–11	IDFdk4	1385–2009	68	0.74	0.72
Tatlayoko Lake	TL	51°51′17″	124°36′23″	1048	2010–11	IDFdk4	1544–2010	59	0.68	0.78
Farwell Canyon	FC	51°50′53″	122°30′51″	898	2010–11	IDFxm	1490–2009	57	0.77	0.56
Site 1	SI	52°01′12″	121°45′0″	900	UBC	IDFdk3	1523–1994	42	0.85	0.77
Site 2	S2	51°52′12″	121°55′12″	1050	UBC	IDFdk3	1491–1995	43	0.74	0.73
Site 5	S5	51°39′0″	121°52′48″	1129	UBC	IDFdk3	1632–1995	31	0.79	0.74
Site 6	S6	51°28′48″	121°49′12″	1285	UBC	IDFdk3	1437–1994	40	0.80	0.76
Meadow Lake	ML	51°24′34″	121°55′43″	1171	2010–11	IDFdk3	1516–2010	50	0.76	0.66
Chasm	CM	51°12′25″	121°28′16″	1055	2010–11	IDFxw-dk3	1458–2010	71	0.74	0.72
Non-host										
Regional lodgepole pine	PL	51–52°	122–124°	985–1280	PFC, UBC	IDFdk-SBPSxc	1775–2011	233	0.54	0.81
Regional ponderosa pine	PY	50–52°	119–121°	700–1113	ITRTB , UBC, UVTRL	BGxw-PPxh	1576–2011	95	0.62	0.74

[a] Source: 2010–11 = this study; ITRDB = International Tree-Ring Database; PFC = Alfaro et al. (2004); UBC = Daniels and Watson (2003); UVTRL = Campbell et al. (2005, 2006).
[b] Biogeoclimatic abbreviations: BG = Bunchgrass, IDF = Interior Douglas-fir, PP = Ponderosa pine; dk = dry-cool, xm = very dry-mild, xw = very dry-warm.
[c] First order autocorrelation.

relatively constant variance (Cook and Kairiukstis, 1990). The ring-width series were standardized using a two-step process: (1) a negative exponential curve that removed biological growth trends; and, (2) 50-year 50% frequency response cubic spline (Cook and Peters, 1981).

The relationship between climatic variables (average temperature (°C) and total precipitation (mm)) and tree-growth of the host and non-host chronologies was evaluated using the program R (R Development Core Team, 2013) package *bootRes*, which computes Pearson correlation coefficients and uses bootstrapping to calculate significance and confidence intervals (Zang, 2012; Zang and Biondi, 2012). Correlation coefficients were computed between residual chronologies and homogenized temperature (Vincent et al., 2012) and adjusted precipitation (Mekis and Vincent, 2011) data from the Adjusted Historical Canadian Climate Database (http://www.ec.gc.ca/dccha-ahccd/) for the Kamloops, Williams Lake and Tatlayoko Lake stations (Table 3). Correlation coefficients were computed on monthly climate variables from the previous June ($t-1$) to September of the current growing year (t) in order to determine the significance of the previous growth season climate on tree growth in the current year (Fritts, 1976).

The tree-ring program OUTBREAK was used to reconstruct WSB outbreaks by applying a set of user-defined criteria for identifying sustained growth reductions in each site chronology, and thus potential insect-outbreak periods (Holmes and Swetnam, 1996). Individual host chronologies, comprised of standardized ring-width series averaged per tree, from each site were corrected separately using the regional non-host chronology using the following criteria: (1) a minimum threshold of 8 years of below-average growth; (2) reduction in growth below −1.28 standard deviation (representing the lowest 10th percentile in growth); and, (3) inclusion of periods of growth release prior to and after the maximum growth reduction, to allow for the potential of increased growth years at the beginning and ending years of an outbreak when larval populations may be fluctuating (i.e., declining and then surging) (Swetnam et al., 1995; Ryerson et al., 2003). Similar threshold parameters were previously used to identify WSB outbreaks (Swetnam and Lynch, 1989, 1993; Swetnam et al., 1995; Campbell et al., 2005, 2006; Alfaro et al., 2014). WSB reconstructions were developed with both the regional ponderosa and lodgepole pine non-host chronologies over the common period (1775–2011) and correlated to ascertain the degree of fidelity between the two reconstructed outbreak histories.

Evaluation of historical WSB outbreaks at each site required a minimum sample-depth. Accordingly each outbreak reconstruction was truncated at a minimum of four trees. Outbreak number, duration and return intervals were summarized for each site, and averaged across sites. Return intervals were calculated from the start of one outbreak to the start of the next outbreak. Three thresholds were used that correspond to light, moderate and severe defoliation: (a) at least 15% of trees recording an outbreak (light), which minimizes noise but is more inclusive of lower intensity outbreaks; (b) at least 50% of trees recording an outbreak (moderate); and, (c) at least 75% of trees recording an outbreak (severe).

To evaluate the robustness of the reconstructed outbreak history we compared those occurring in the latter half of the 20th century with documented outbreaks in the southern interior of BC (Harris et al., 1985; Erikson, 1992) and with those identified in recent provincial aerial overview surveys (Westfall and Ebata, 2000–2011). Our reconstructions were also compared to previous multi-century WSB outbreak reconstructions at sites in the southern BC interior (Campbell et al., 2005, 2006; Alfaro et al., 2014) and in the northwestern US (Swetnam et al., 1995; Flower et al., 2014).

In addition to assessing WSB outbreaks using the ratio of trees that record an outbreak, the corrected chronologies were also examined to describe the integrated stand-level response to WSB outbreaks. All of the corrected chronologies were truncated to the year 1632 and correlated to one another using Pearson correlation coefficients. Data were then transformed using a 10-year spline to reduce inter-annual variability while still maintaining high-frequency variability in the time series. All of the smoothed corrected indices were grouped on the basis of their correlation coefficients and averaged into sub-regional chronologies to create outbreak histories within the larger study area.

While it was not the primary objective of this study, we examined possible relationships between synchronous outbreaks and climate by comparing the sub-regional chronologies with independently reconstructed summer temperature (June–August) and May 1 snow water equivalence (SWE) anomalies for the Tatlayoko Lake station (Table 3; Starheim et al., 2012). To facilitate comparison between the datasets, the reconstructed climatic anomalies were transformed using a 10-year spline. Synchronous WSB outbreaks were defined as periods when >5 consecutive years had index values in the lowest 75% percentile in at least 3 of the 4 sub-regional chronologies.

Table 2
Characteristcs of the biogeoclimatic units where chronologies were sampled. Adapted from Steen and Coupé (1997).

Interior Douglas-fir (IDF)	Biogeoclimatic units			
	xw	xm	dk3	dk4
BEC unit label	Very dry-warm	Very dry-mild	Dry-cool Fraser	Dry-cool Chilcotin
Elevation (masl)	600–1000	800–1200	750–1200	1050–1350
Area (km^2)	362	2373	8953	3994
Location in Cariboo Forest Region	Southeast corner	Valleys of the Fraser and Chilcotin rivers	Southeast to northwest (Williams Lake), east of the Fraser River valley	North and south of the Chilcotin and Chilanko river valleys
Mean annual precipitation (mm)	No data	392	433	355
Mean annual temperature (°C)	3.5	4.0	3.3	2.8
General description	Open park like appearance, with mixed ponderosa pine and little to no regeneration	Parkland of grasslands and Douglas-fir forests, some clumps of aspen	Multi-aged Douglas-fir forests with abundant but clumpy regeneration	Coldest variant of IDFdk subzone in province, lodgepole pine present where there is cold air accumulation
Dominant herb layer	Pinegrass; Bluebunch wheatgrass	Pinegrass; Kinnikinnick	Pinegrass; Twinflower	Pinegrass; Kinnikinnick
Adjacent BEC zones[a]	Above PP	Above BG below IDFdk	Above the IDFxm and below SBPS/MS	Below SBPS

[a] Biogeoclimatic abbreviations: PP = Ponderosa Pine, BG = Bunchgrass, SBPS = Sub Boreal Pine Spruce, MS = Montane Spruce.

Table 3
Climate station name, ID number, period of record, location and elevation.

Climate station	Station ID	Period	Latitude	Longitude	Elevation (masl)	Correlated host-chronologies
Kamloops	1163780	1890–2010	50°42′08″	120°26′31″	345	S5, S6, ML, CM, PY
Tatlayoko Lake	1088015	1930–2010	51°42′01″	124°24′02″	870	TL
Williams Lake	1098940	1939–2010	52°12′01″	122°05′59″	940	FR, BC, RS, FC, S1, S2

Wavelet analysis was performed to decompose the sub-regional chronologies into time–frequency domains to identify the dominant modes of variability through time (Torrence and Compo, 1998). Wavelet analysis was performed using a continuous Morlet transformation at the 99% confidence level on the sub-regional chronologies in the R package *dplR* (Bunn, 2008; Bunn et al., 2012).

3. Results

3.1. Tree-ring data

The tree-ring chronologies used in this study were collected at sites found throughout the study area (Fig. 1). Fourteen archived and newly collected Douglas-fir chronologies sites were combined to develop 11 host chronologies (Table 1). Six archived lodgepole pine chronologies and 6 archived ponderosa pine chronologies were combined to develop two regional non-host chronologies (Table 1).

The Douglas-fir chronologies were constructed from trees found primarily in the dry-cool Fraser or the dry-cool Chilcotin BEC units, with the exception of the Fraser River and Farwell Canyon chronologies constructed from trees located in the very dry-mild BEC unit (Tables 1 and 2). Two chronologies were located in transitional BEC units: the Bull Canyon chronology is transitional between very dry-mild and dry-cool Chilcotin; in the southeast the Chasm chronology is transitional between the very dry-warm and dry-cool Fraser (Fig. 1; Tables 1 and 2). All the Douglas-fir sites were characterized by open forests (averaging 375 trees per hectare) where the drier stands (very dry-mild and very dry-warm) represent a transition from grassland to more continuous forest at higher elevations (dry-cool BEC units) (Steen and Coupé, 1997). Douglas-fir sites were located on rolling to terraced terrain, predominantly on south to southwest facing slopes with elevations ranging from 600 to 1285 masl (Table 1). The chronologies collected for this study (2010 and 2011) came from trees exhibiting current WSB defoliation, as well as evidence of previous outbreaks, such as top-kill and sparsely foliated crowns.

The regional lodgepole pine chronology was compiled from sites located in the dry-cool Fraser or dry-cool Chilcotin BEC units or adjacent BEC units (e.g., Sub-Boreal Pine Spruce) (Table 1). Stands were composed predominately of lodgepole pine with minor components of veteran Douglas-fir and/or aspen (*Populus tremuloides* Michx.). Lodgepole pine stands typically had a higher density than the Douglas-fir sites (around 800–900 trees per hectare), and were located on mainly flat to rolling terrain with elevations ranging from 985 to 1280 masl (Table 1).

The regional ponderosa pine chronology was compiled from sites in the southern portion of the study area, at the northern range of the species distribution (Burns and Honkala, 1990), or from the adjacent Thompson–Okanagan Forest Region (Fig. 1). Stands were located in the Bunchgrass or Ponderosa pine BEC units, where the climate is characterized by warm to hot, dry summers and moderately cold winters with little snowfall (Steen and Coupé, 1997). Ponderosa pine stands were mixed with Douglas-fir and characterized by open forests (averaging 270 trees per hectare) with the understory dominated by pinegrass (*Calamagrostis rubescens* Buckl.) located on slopes with variable aspects (Table 1).

3.2. Dendrochronological characteristics

The Douglas-fir trees sampled in this study averaged 494 years in age (Table 1), while the ponderosa and lodgepole pines ranged in age from 236 to 435 years, respectively (Table 1). Inter-serial correlation (r), the variation in tree-ring growth among all sampled trees in a stand, ranged between 0.68 and 0.85 in Douglas-fir and from 0.54 to 0.62 in the non-host chronologies, demonstrating that

all three species record a strong commonality in the response to environmental influences. First-order autocorrelation, common in tree-ring series describes the correlation between the tree-ring width in the previous year (*t-1*) and ring width in the current year (*t*) (Fritts, 1976). In Douglas-fir, the lag-1 autocorrelations ranged from 0.49 to 0.78 and the non-hosts were 0.74–0.81, indicating the strong influence of radial growth in the previous year growth on current year's growth (Table 1).

Pearson correlation coefficients between residual chronologies and mean temperature and total precipitation indicate that both host and non-host radial growth was similarly affected by climate (Table 4). The most consistent significant correlations in all of the chronologies occurred for previous August precipitation ($t-1$) and, to a lesser extent, previous June precipitation (Table 4). Significant correlations to mean monthly temperatures tended to be sporadic and no strong pattern emerged across sites (Table 4).

3.3. Outbreak reconstructions

Initially we developed two sets of outbreak reconstructions, one constructed using the regional lodgepole pine chronology as the non-host and a second constructed using the regional ponderosa pine chronology as the non-host. The average correlation coefficient between the reconstructions was 0.60 (ranging from 0.42 to 0.83) (Fig. 2a), indicating good correspondence between non-hosts and providing confidence that either could be used in the outbreak analyses. The outbreak reconstructions for each non-host are plotted for Site 5 (Fig. 2b), which had an average correlation coefficient between reconstructions ($r = 0.58$), illustrating that overall the two non-hosts produced similar outbreak histories in terms of timing and duration. The most significant difference between the two reconstructions was the outbreak intensity. Reconstructions based on lodgepole pine generally had a higher ratio of trees meeting the outbreak parameters than those based on ponderosa pine (e.g., Fig. 2b). This pattern was consistent for all sites suggesting that WSB outbreak reconstructions based on ponderosa pine are likely to be more conservative. Nonetheless, we chose to use only the regional ponderosa pine chronology to construct our final WSB reconstruction as it extended further back in time (>400 years).

Our WSB reconstructions show that outbreaks have occurred in the Cariboo Forest Region for the past 300–400 years (Fig. 3). These outbreaks have varied in intensity and duration at individual sites, but at times were highly synchronous across the study area (Figs. 3 and 5). The sites with the longest outbreak reconstructions (FR, RS, FC, S6, ML and CM; Table 1) all recorded outbreaks in the early-1600s and 1630s, where 80–100% of trees recorded outbreaks (Fig. 3). From the 1650s to the early-1700s site-specific outbreaks occurred at generally low levels. In the 1720s a synchronous, moderate outbreak occurred at all sites (Fig. 3). In the 1770s a high intensity (60–80% of trees) outbreak occurred at nearly all the sites, with the exception of FC and S1 (Fig. 3). The 1800s were characterized by a period of predominately stand-specific outbreaks of variable intensity until the late-1800s when all the sites recoded a severe outbreak (80–100% of trees) (Fig. 3).

Our reconstructed outbreak history was compared with survey records from the 20th and 21st centuries. Ninety-one percent of the Douglas-fir stands examined in this study record outbreaks from the late-1930s to mid-1940s (Fig. 3). Although few records exist in the study area prior to 1994, documented outbreaks in the mid-1930s to mid-1940s to the south and west closely coincide to our reconstructed outbreaks (Harris et al., 1985). The 1974 WSB outbreak observed by Erikson (1992) near the FC site chronology (Fig. 1) appears at 64% of our sites, albeit as a low intensity event that impacted from 20% to 40% of the trees at sites recording the outbreak (Fig. 3). All of the sites recorded outbreaks in the mid-1990s (Fig. 3), and by the mid-2000s 80 to 100% of trees at all sites recorded the outbreak events mapped by the provincial aerial overview survey (Westfall and Ebata, 2000–2011).

Table 4
Significant Pearson correlation coefficients ($p < 0.05$) between current residual tree-ring chronologies and climate variables in the growth seasons prior to (*italics*) and concurrent with ring formation.

Site ID	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Mean temperature (°C)																
FR			*−0.29*													
BC						*-0.24*					0.23		−0.22	−0.22		
RS											0.26					
TL			*0.27*	*0.30*				0.24					0.31			
FC													−0.25			
S1	*−0.31*															
S2																
S5										−0.18						
S6																
ML						*−0.18*										
CM																
PL													−0.26			
PY											0.19					
Total precipitation (mm)																
FR			*0.40*	*−0.25*								0.22				
BC			*0.33*						−0.21							
RS			*0.32*	*−0.25*						0.26		0.35				
TL			*0.23*													
FC			*0.36*													
S1	*0.36*			*−0.26*								0.45				0.26
S2			*0.44*	*−0.27*										0.27		
S5			*0.48*							−0.21						−0.33
S6	*0.17*		*0.34*													−0.33
ML	*0.21*		*0.42*	*0.21*												−0.24
CM	*0.23*		*0.34*	*0.19*									0.20		−0.18	−0.22
PL			*0.51*	*−0.23*												
PY			*0.43*	*0.33*									0.24			

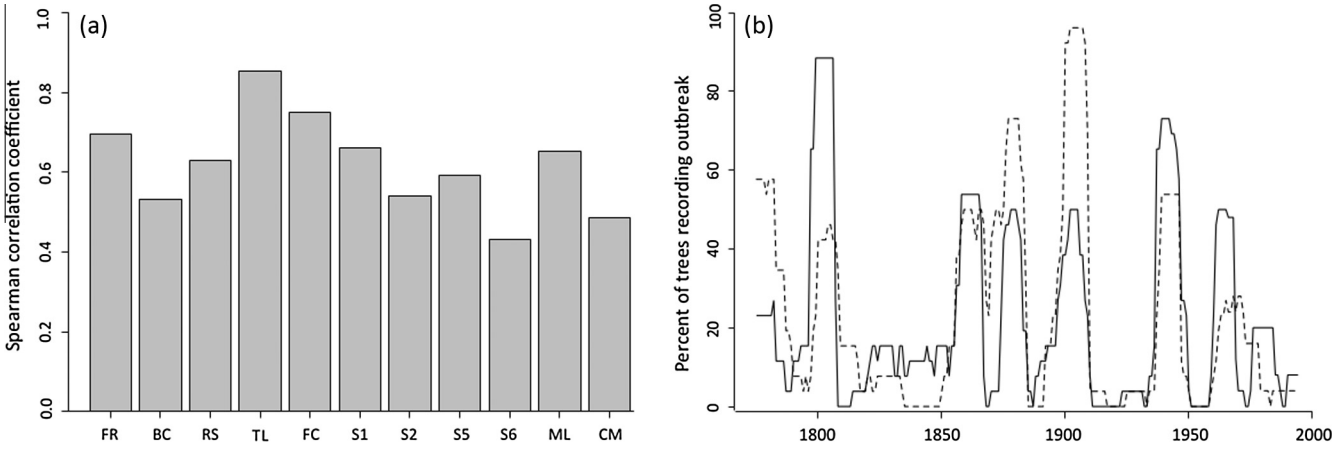

Fig. 2. (a) Pairwise Pearson correlation coefficients between reconstructions of western spruce budworm outbreaks computed using the regional non-host lodgepole pine chronology (PL) and the regional non-host ponderosa pine chronology (PY); all correlations are significant ($p < 0.05$). (b) An example of western spruce budworm reconstructions for Site 5 (S5) using PL (solid line) and PY (dashed line).

Table 5 summarizes the reconstructed outbreak history by number, duration and return interval for light, moderate and severe defoliation periods. The greatest number of outbreaks corresponded to light defoliation, and the least to severe defoliation events. In the light defoliation category we reconstructed an average of 12 outbreaks with an average duration of 15 years (±1.8 years) and a return interval of 29.8 years (±5.6 years) (Table 5). For moderate defoliation there was an average of 5 outbreaks with an average duration of 11 years (±5.5 years) and return interval of 64.2 years (±20.2 years). Under the severe defoliation category there was an average of 2 outbreaks, with an average duration of 9.6 years (±1 year) and a return interval of 132.8 years (±44.5 years) (Table 5).

Pairwise Pearson correlation coefficients between corrected chronologies showed that the highest *r* values occurred between chronologies located within the same, or adjacent BEC units (Tables 1 and 6). All corrected chronologies, smoothed with a 10-year spline and grouped on the basis of their correlations coefficients, resulted in four sub-regional chronologies that correspond to BEC units across the study area. One group included the FR and FC chronologies from the very dry-mild BEC unit; another group included the northern chronologies, BC, RS and TL located in the dry-cool Chilcotin BEC unit; a third group included the S1, S2, S5 and S6 chronologies from sites east of the Fraser River valley in dry-cool Fraser unit; and, the final group included the two southernmost chronologies, ML and CM, which are transitional between the dry-cool Fraser or the very-dry warm BEC units, respectively (Fig. 4).

3.4. Outbreaks and climate

From 1658 to 2009, smoothed records of Tatlayoko Lake summer temperature (June–August) and May 1 snow water equivalence (SWE) highlight the low frequency variability inherent to each time series (Fig. 5a and b). Positive summer temperature anomalies are generally accompanied by negative May 1 SWE anomalies (and vice versa), although this strong inverse relationship weakens in the 1840s until the late-1880s, when the amplitude of anomalies flattens (Fig. 5a and b). The decreased amplitude in the summer temperature record is particularly notable and lasts from around the mid-1700s to late-1800s (Fig. 5a). From 1658 to 2009, ten synchronous outbreak periods at the sub-regional scale were identified (Fig. 5c). In general, synchronous outbreaks at the beginning and end of the record correspond to positive summer temperature and negative SWE anomalies (Fig. 5). However, the opposite trend occurs from the late-1700s to the 1850s and late-1920s when synchronous outbreaks corresponded to negative temperature and positive SWE anomalies. From the early-1800s to the 1860s there is an absence of synchronous outbreaks in sub-regional chronologies and a decomposition in a common signal between chronologies (Fig. 5c), which corresponds to decreased amplitude in summer temperature anomalies over the same period (Fig. 5).

3.5. Periodicity of outbreaks

Wavelet analysis revealed both high and low frequency variability in the WSB sub-regional chronologies (Fig. 6). The high frequency ~16-year period is apparent in each sub-regional chronology primarily from the 1670s to approximately the late-1700s to early-1800s. This mode of variability appears associated with high frequency oscillations in the sub-regional chronologies, which is most pronounced in the dry river valley sites of the very-dry mild BEC unit, and is nearly absent in the wetter forests of the dry-cool Fraser unit (Fig. 6; Table 2). The low-frequency, multi-decadal signal centered on the 32-year period is a prominent feature in all of the sub-regional chronologies after the late-1700s and likely reflects more regular WSB outbreaks across the study area (Figs. 3 and 6). This low-frequency signal is the most prominent signal from the 1850s to present day. In the dry-cool Fraser sub-regional chronology, the wettest BEC unit in the study area (Table 2), and to some extent the transitional dry-cool Fraser to very-dry warm sub-regional chronology, there appears to be a quiescent phase in outbreak behavior from around 1725 to 1825 characterized by lower amplitude oscillations and lower power in the wavelet spectrum in the 32-year period (Fig. 6).

4. Discussion

Reconstruction of western spruce budworm dynamics in the Cariboo Forest Region indicates that outbreaks have been widespread and synchronous over the last four centuries. Over the period of record from 1576 to 2011 we identified 12 low-intensity outbreaks lasting on average 15 years with a return interval of 29.8 years (Table 5). This finding confirms that the outbreaks observed over the last 40 years in this region are not unprecedented and offers no support for the perception that the WSB has been expanding northward into the Cariboo Forest Region.

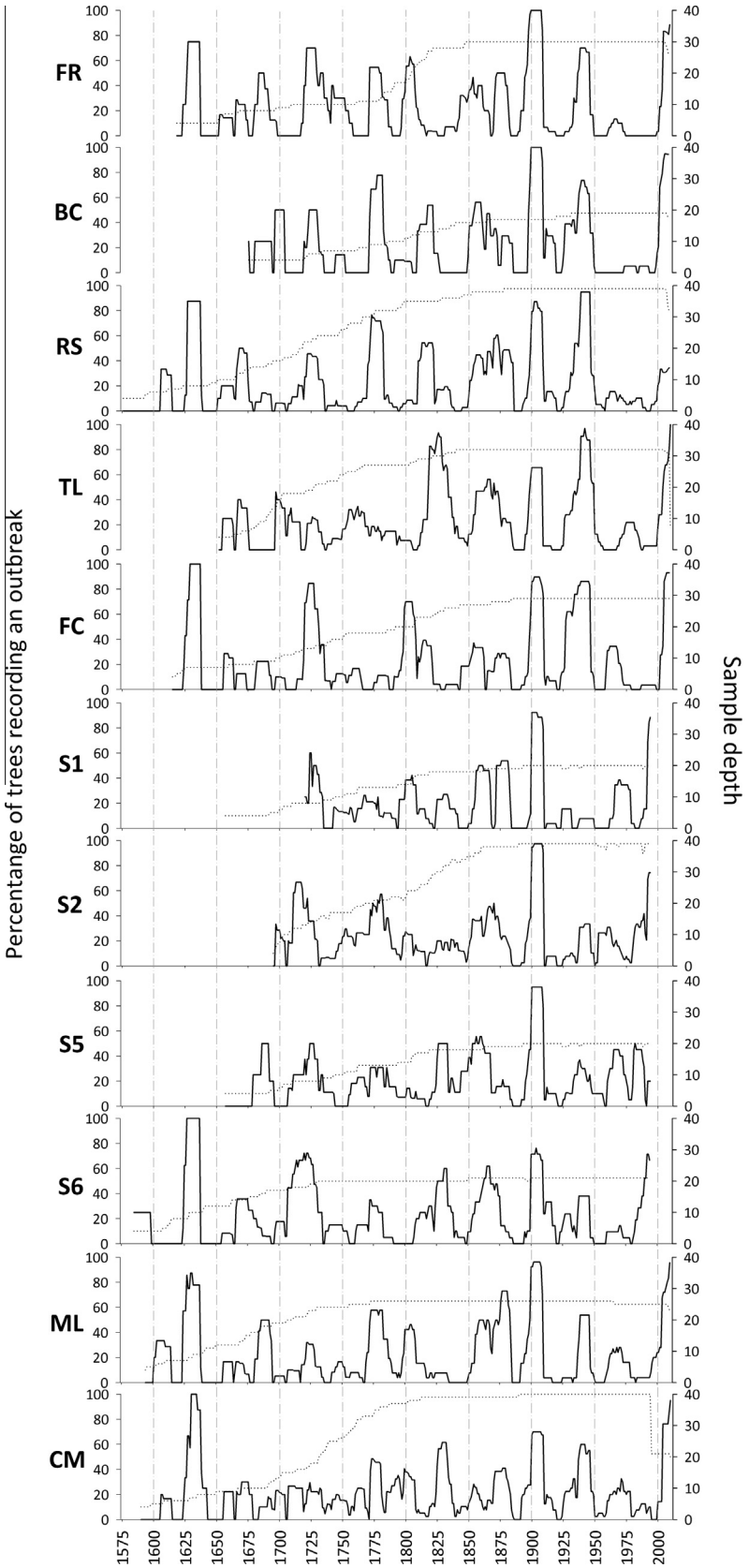

Fig. 3. Reconstructions of western spruce budworm outbreaks across the Cariboo Forest Region, British Columbia, Canada. Outbreak reconstructions were truncated to a minimum sample depth of four trees. Left *y*-axis is the percentage of trees recording an outbreak; right *y*-axis sample depth for each site.

Swetnam and Lynch (1993) describe limitations inherent to tree-ring based reconstructions of WSB outbreaks that are worth considering in the context of our study: (1) only surviving trees are sampled thus reconstructed outbreaks do not capture mortality; (2) non-host species used to correct for climatic variations are themselves imperfect recorders of climate, therefore the corrected chronologies likely contain year-to-year variation unrelated to budworm activity; and (3) identification of budworm outbreaks may be limited to moderate and severe outbreaks as low intensity periods of defoliation may not be readily distinguishable from other forms of variability in the corrected chronologies. Another possibility is that false outbreaks are reconstructed in the corrected tree-ring chronologies, however we find this unlikely as crown defoliation must reach around 50% before significant radial growth losses are detected (Alfaro et al., 1982).

In this study we used two regional non-host controls and found that, for the common period, the reconstructed outbreaks had high fidelity in terms of timing, duration and frequency (Fig. 2). Sources of inconsistency between the two reconstructions were associated with the start and end years of outbreaks, a broad problem with the outbreak detection method employed here due to lag effects between budworm defoliation and subsequent growth suppression (Thomson and van Sickle, 1980; Alfaro et al., 1982; Swetnam and Lynch, 1989) and in the intensity of individual outbreaks. For example, outbreak reconstructions using the regional lodgepole pine non-host show a higher intensity outbreak in the 1800s than the ponderosa pine non-host, while the reverse was true for the 1900s outbreak (Fig. 2b). We attribute these differences to the degree and type of climatic variability captured by each non-host (limitation 2 identified above), as well as the potential for local endogenous processes to be reflected in the year-to-year variation in the tree-ring series.

Using the longer regional ponderosa pine non-host chronology (Table 1), we identified 12 low-intensity WSB outbreaks over a

Table 5
Reconstructed number, duration and return interval of outbreaks by individual sites organized by their sub-regional biogeoclimatic unit grouping. Return intervals are given for three levels of budworm outbreak intensity.

Site	Start of record[a]	Percent of trees affected (%)[b]	No. of outbreaks	Duration (years)		Return Interval[c] (years)	
				Mean	SD	Mean	SD
Very dry-mild (xm)							
FR	1619	15	10	18	12	38	21
		50	9	11	10	42	22
		75	2	11	1	189	115
FC	1615	15	11	14	6	34	7
		50	5	13	4	76	28
		75	4	10	3	94	61
Dry-cool Chilcotin (dk4)							
BC	1676	15	9	16	6	35	19
		50	7	8	2	44	11
		75	2	8	4	113	13
RS	1576	15	13	14	8	30	15
		50	6	27	43	61	48
		75	3	9	2	156	165
TL	1652	15	12	15	9	29	13
		50	4	11	5	47	14
		75	2	9	1	95	35
Dry-cool Fraser (dk3)							
S1	1720	15	11	12	5	21	8
		50	4	8	3	67	56
		75	1	10	–	93	–
S2	1695	15	11	17	13	28	18
		50	3	9	4	94	28
		75	1	10	–	–	–
S5	1657	15	11	15	6	27	14
		50	5	7	2	54	33
		75	1	10	–	–	–
S6	1585	15	12	16	8	33	14
		50	5	11	5	73	35
		75	1	11	–	–	–
Very dry-warm (xw)							
ML	1594	15	12	16	12	33	19
		50	7	9	3	54	29
		75	2	10	1	190	117
CM	1590	15	19	13	6	20	9
		50	4	9	2	94	72
		75	1	8	–	–	–
Average	1634	15	12	15.1	1.8	29.8	5.6
		50	5	11.2	5.5	64.2	20.2
		75	2	9.6	1.0	132.8	44.5

[a] Start of record for each site truncated when there were fewer than four host trees in the sample.
[b] Percent of trees equates to defoliation intensity: low > 15%, moderate > 50% and severe > 75%.
[c] Return intervals are number of years between start year of outbreaks.

Table 6
Significant pairwise correlation coefficients ($p < 0.01$) between corrected chronologies. For each chronology the highest between-sites correlation coefficient is outlined.

	FR	BC	RS	TL	FC	S1	S2	S5	S6	ML	CM
FR	1	0.672	0.566	0.396	0.740	0.545	0.479	0.515	0.485	0.703	0.609
BC		1	0.689	0.567	0.623	0.448	0.524	0.483	0.472	0.583	0.602
RS			1	0.704	0.659	0.594	0.609	0.631	0.613	0.527	0.533
TL				1	0.465	0.506	0.549	0.569	0.572	0.437	0.489
FC					1	0.615	0.61	0.622	0.606	0.589	0.482
S1						1	0.655	0.659	0.604	0.438	0.401
S2							1	0.776	0.746	0.497	0.480
S5								1	0.799	0.531	0.585
S6									1	0.505	0.572
ML										1	0.731
CM											1

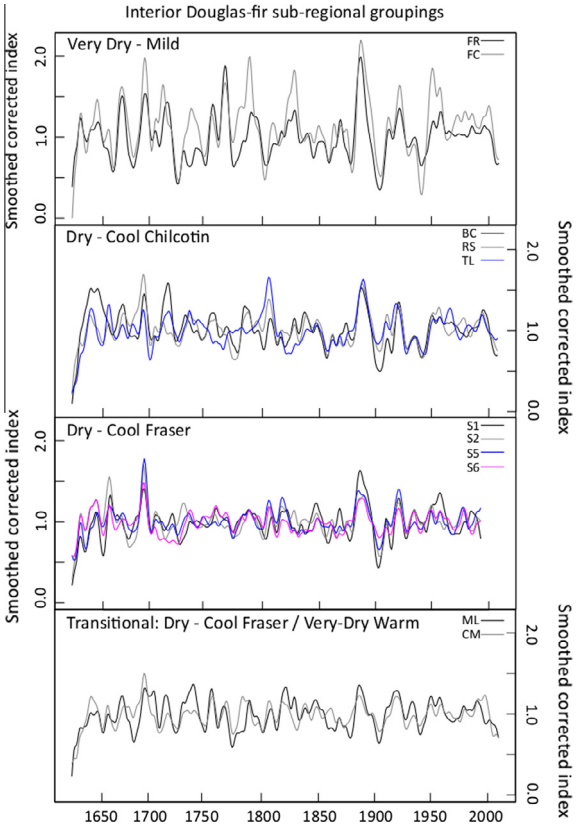

Fig. 4. Smoothed (10-year spline) sub-regional chronologies plotted by biogeoclimatic unit. Start year truncated to 1632 and end year to 1994 for dry-cool Fraser sites and to 2009 for remaining sites (see Tables 1 and 2 for chronology abbreviations and biogeoclimatic unit descriptions).

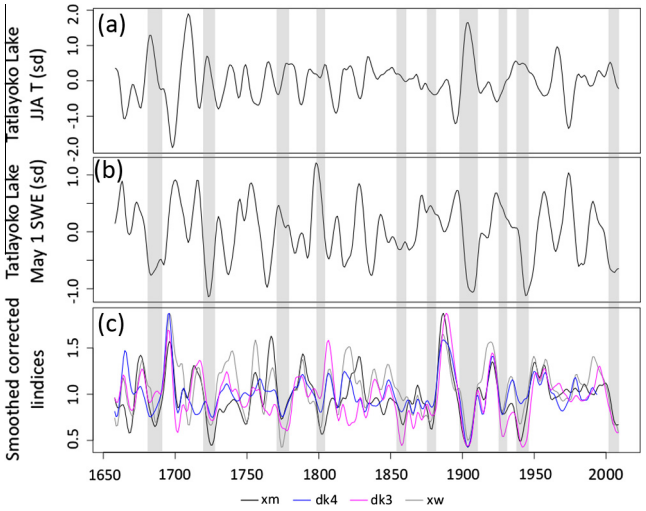

Fig. 5. Relationship between reconstructed climatic variables (a & b; Starheim et al., 2012) and sub-regional western spruce budworm outbreak reconstructions (c) smoothed with a 10-year spline: (a) Tatlayoko Lake June–August temperature (JJA T) anomalies (sd = standard deviation); (b) Tatlayoko Lake May 1 snow water equivalence (SWE) anomalies; (c) sub-regional reconstructions (xm = very dry-mild, dk4 = dry-cool Chilcotin, dk3 = dry-cool Fraser, xw = very dry-warm). Grey shading corresponds to synchronous outbreak periods representing index values in the lowest 75% percentile for each sub-regional outbreak reconstruction.

435-year period, or one outbreak approximately every 36 years. This finding is similar to those of Campbell et al. (2006) who identified 8 WSB outbreaks over a 300-year period or one outbreak approximately every 37 years in the southern interior of BC. While we identified low-intensity events when ⩾15% of trees recorded an outbreak, Campbell et al. (2006) identified an outbreak when ⩾35% of trees recorded an outbreak (Table 5).

The application of a minimum threshold can be effective at differentiating between low and moderate intensity outbreaks. However, the threshold itself is somewhat subjective, as it is not based on theoretical or experimental values. It is possible that the threshold minimum of 35% may be too conservative and exclude small and/or low intensity events (Ann M. Lynch, *personal communication*). Defoliation impacts are often highest among trees in the suppressed and intermediate height classes (Alfaro and Maclauchlan, 1992), yet in our study (and others) canopy dominants were selected for reconstruction purposes to obtain the longest possible records. These individuals, however, may not be capturing the full impact of budworm feeding. When we increased the minimum threshold to 50% (moderate) the number of reconstructed outbreaks dropped to 5 (from 12) that on average lasted 11 years with a return interval of 64 years (Table 5). While the duration of low and moderate intensity events were similar (15 *versus* 11 years), the return interval increased two-fold (Table 5), which is consistent with return intervals reconstructed for WSB outbreaks in the Colorado Front Range (Ryerson et al., 2003).

Examining the corrected chronologies at the sub-regional scale provides another avenue to explore WSB outbreak dynamics across the study area, and illustrates the strong association between chronologies collected from the same BEC units (Fig. 4). The sub-regional chronologies highlight the strong fidelity between chronologies within group (i.e., BEC unit) and the synchronous WSB outbreak events across the study area, while also emphasizing the unique outbreak history at smaller spatial scales (Figs. 4 and 5). For example, chronologies in the very dry-mild BEC unit (FC and FR) are located on south facing slopes of the Fraser or Chilcotin Rivers

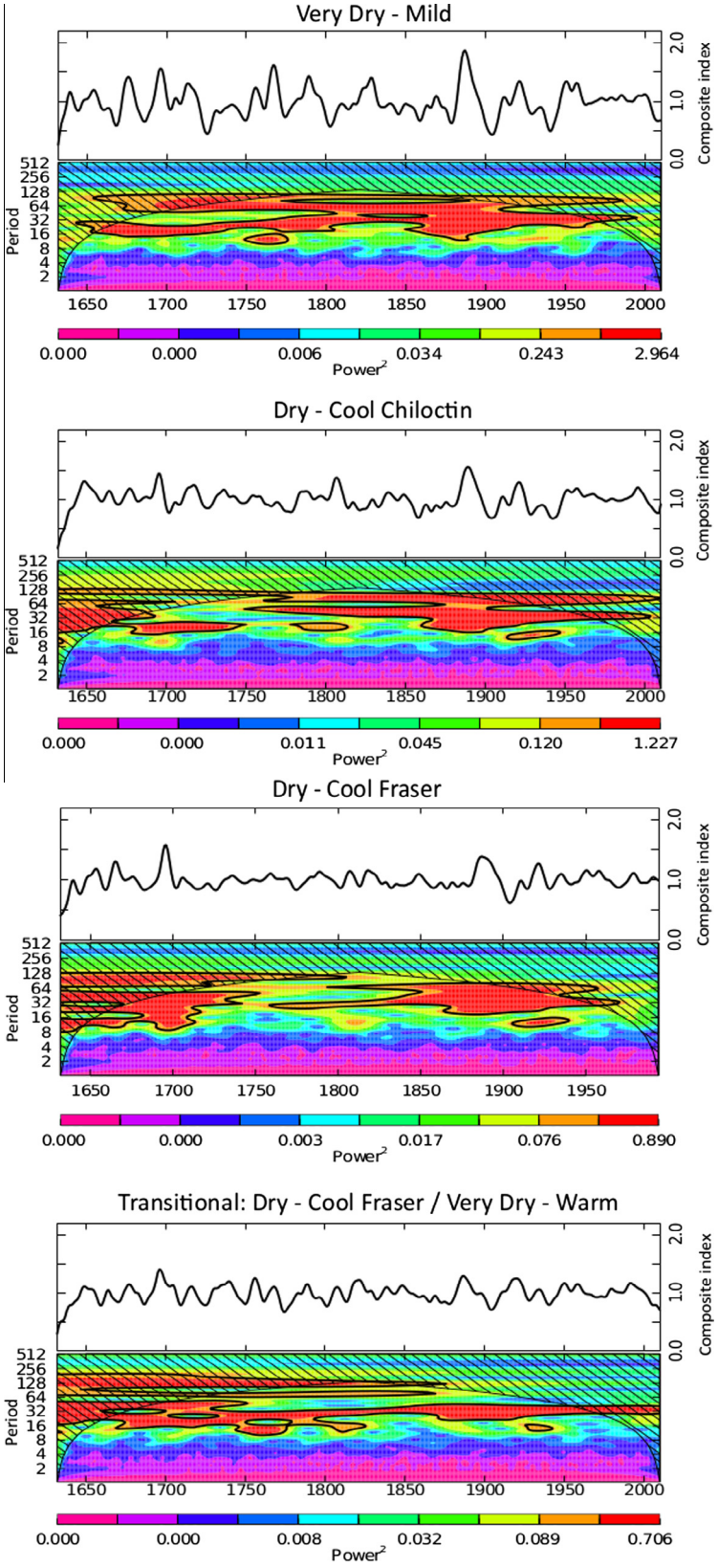

Fig. 6. Sub-regional chronologies smoothed with a 10-year spine (top panel) and the wavelet power spectrum based on a continuous Morlet transformation (bottom panel). The cross-hatched region in lower panel of each plot is the cone of influence, where zero padding has reduced the variance, and the black contour encloses regions of greater than 99% confidence.

and were characterized by a pronounced high amplitude signal when compared to the other sub-regional chronologies (Fig. 4). Chronologies from the dry-cool Fraser BEC unit (S1–S2, S5–S6) (Fig. 4), which is characterized by wetter and cooler conditions, have a notable quiescent phase from the early-1700s to early-1800s (Figs. 4 and 5) that also corresponds to decreased power in the wavelet spectrum (Fig. 6). This suggests that site and/or stand conditions play an important role in mediating tree response to WSB outbreaks. For the very dry-mild sites conditions such as steep slopes, thin soils, and availability of soil moisture all likely contribute to increasing the sensitivity of these chronologies to negative (e.g., WSB defoliation) and positive (e.g., growing season moisture) stimulus. Conversely, the dry-cool Fraser sites, which were sampled at higher elevation (Table 1) and not from steep slopes, have a dampened sensitivity to environmental factors (Fig. 4). Site factors in combination with cooler and wetter climatic conditions (Table 2) are likely resulting in a more average growth response over time where tree grow is less responsive to events like budworm feeding (Fig. 4). The stand level to sub-regional scale WSB outbreak dynamics across the study area highlight the complex interactions between: site characteristics, canopy structure and composition, host plant quality, bud phenology, growth rates, tree resistance and climate, which to some extent all play a role in determining the intensity of individual outbreaks and tree growth responses across an area (Kozlowski, 1969; Clancy, 1992; Swetnam and Lynch, 1993; Chen et al., 2001; Maclauchlan and Brooks, 2009; Nealis, 2012).

Synchronous outbreak periods in the Cariboo Forest Region in the 1720s, late-1700s, 1870s and 1930s (Fig. 5) were also present in the reconstructions from locations south of our study area (Campbell et al., 2005, 2006; Alfaro et al., 2008, 2014; Flower et al., 2014). Notably, the outbreak from 1898 to 1909 was a widespread event that appears in reconstructions in the area directly south of the Cariboo Forest Region (Campbell et al., 2006; Alfaro et al., 2014), the southern Okanagan (Alfaro et al., 2008, 2014), southern Vancouver Island (Harris et al., 1985), as well as in northeastern Oregon (Swetnam et al., 1995) and in stands found from central Oregon to western Montana (Flower et al., 2014). Three mechanisms have been suggested for coincident changes in the abundance of geographically discrete populations: dispersal of populations; dependence of population dynamics on a synchronous exogenous factor such as temperature or rainfall, essentially the "Moran" effect (Moran, 1953); and, trophic interactions with populations of other species that are also spatially synchronous or mobile (Liebhold et al., 2004). Peltonen et al. (2002) studied spatial synchrony of forest insect outbreaks found that the Moran effect was likely the dominant mechanism causing spatial synchrony in outbreaks across regional scales and that dispersal was of lesser importance. This finding was supported by Swetnam and Lynch (1993) who also found that exogenous factors (e.g., climatic variability) played a significant role in regulating regional-scale WSB outbreaks in northern New Mexico. More recently, Flower et al. (2014) found that warm-dry climate preceded outbreaks by up to three years, but during outbreaks conditions tended to be cooler and wetter.

The comparison of regionally synchronous WSB outbreaks and climatic proxies from the western portion of the study area suggest that the influence of climate on outbreak dynamics is highly complex (Fig. 5). From the late-1600s to early-1700s and from the 1940s to the end of the record, synchronous outbreaks coincide with positive summer temperature and negative SWE anomalies indicative of warmer and drier climatic conditions (Fig. 5). However, from the late-1700s to the around the 1920s synchronous outbreaks coincide with negative temperature and positive SWE anomalies that are indicative of cooler and wetter climatic conditions (Fig. 5). During this same time period (with the exception of the 1920s) extensive wet periods prevailed across the southern Canadian Cordillera (Watson and Luckman, 2004) and there were numerous episodes of glacial expansion in Mt. Waddington range west of the study area (Larocque and Smith, 2003). During periods when warmer and drier conditions were associated with WSB outbreaks (Fig. 5), Starheim et al. (2012) found that the low-frequency signals associated ocean-atmospheric forcing, i.e., Pacific Decadal Oscillation and the Pacific North America Index were prominent in their hydroclimatic reconstructions.

Previous research in the western US shows that WSB outbreaks are associated with wetter conditions in the spring and summer, while years leading up to outbreaks are associated with drought conditions (Swetnam and Lynch, 1989, 1993; Ryerson et al., 2003; Flower et al., 2014). In southern BC, outbreaks have been found to be associated with average air temperatures and drier winters (Campbell et al., 2006). Our comparison between reconstructed summer temperature and May 1 SWE anomalies, and synchronous WSB outbreaks reveals that the association of these variables are not temporally stable and suggest that a single climatic condition does not offer an explanation for regionally synchronous outbreaks in the central interior of BC.

In previous studies of WSB outbreak cycles, strong periodic components of ~30 and 40 years over centuries have been documented using Single Spectrum Analysis (Ryerson et al., 2003; Campbell et al., 2006; Alfaro et al., 2014), and are similar to periods found by Swetnam and Lynch (1993). In eastern Canada, eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) populations have oscillated more or less periodically over two centuries with an average period of 35 years (Royama, 1984). In this study, a continuous Morlet wavelet transform of the sub-regional chronologies revealed strong modes of variability ranging from 16 to 64-year cycles (Fig. 6), which is consistent with other studies. The beginning of the outbreak chronologies, early-1600s to mid-1700s, was characterized by the high frequency 16-year pattern suggesting that WSB outbreak occurred with greater frequency during the 15–16th centuries (Fig. 6). The lower-frequency 32-year period became more evident after the late-1700s, which is coherent with the analysis of the return intervals of WSB outbreaks (Table 5) and coincides to the period when cooler and wetter conditions were associated with regionally synchronous WSB outbreaks (Figs. 5 and 6). In all of the sub-regional chronologies this low-frequency 32-year period became prominent after the mid-1850s suggesting that WSB outbreaks became more temporally stable after this time (Fig. 6). Widespread outbreaks across the study area (Fig. 5), and outbreak periodicities with an average of 32-years (Fig. 6) supports previous research that climate may have a synchronizing influence on outbreak dynamics at larger spatial scales (Royama, 1984; Williams and Liebhold, 2000; Peltonen et al., 2002; Jardon et al., 2003). However, more detailed analysis of a variety of climatic parameters is required to corroborate this in our study area.

5. Conclusion

Multi-century reconstructions of WSB outbreaks in the Cariboo Forest Region of British Columbia describe their cyclic population dynamics and demonstrate the long standing presence of WSB in this area. WSB outbreaks have occurred throughout the entire 400-year record at the stand to the regional level, with outbreaks lasting from 14 to 18 years not uncommon. Perhaps most importantly, this study demonstrates that outbreaks observed over the last 40 years in this region are not unprecedented and offers no support for the perception that the WSB has been expanding northward into the Cariboo Forest Region.

Numerous WSB outbreaks documented in this study are synchronous with large-scale events recorded in the southern interior

of BC and in the northwestern US states. Large-scale budworm outbreaks at this spatial scale are likely affected by global processes (e.g., climate), while processes endogenous to the budworm/host relationship (e.g., bud burst phenology) are likely responsible for local variability in timing and intensity of outbreaks. At smaller-scales the relative influences of dispersal and stochastic agents remains uncertain (Peltonen et al., 2002), thus more focused research on the role of endogenous variables, such as the degree of homogeneity in budburst phenology in combination with measures of budworm population rates of change, and/or severity of defoliation could provide more direct linkages between weather, host-plant relationships, and outbreak dynamics (Nealis and Nault, 2005).

This research fills an important knowledge gap on the spatial temporal dynamics of WSB outbreaks in the central BC, close to the edge of the distribution of its host, Douglas-fir. The current sustained outbreak in the Cariboo Forest Region is not yet unprecedented when considering the last 400 years, however additional research is required to gain a better understanding of the long-term WSB dynamics to the north and east of our study area. At the stand and tree-level, research directed at quantifying what minimum thresholds are biologically meaningful to identify historical outbreaks would be useful, as would gaining a more detailed understanding of how local factors (e.g., bud burst phenology and insect dispersal) control outbreak initiation and defoliation severity and duration. A detailed analysis of how climate influences widespread outbreaks in the central interior of BC is required to determine how this compares or contrasts with results obtained from other regions of western North America. Finally, climate change is expected modify insect-host relationships; where the intensity of insect outbreak behavior is expected continued attention needs to be directed at questions such as how intrinsic population growth is related to temperature and how dispersal is altered by climate change.

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References

Alfaro, R., Maclauchlan, L., 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., Van Sickle, G., Thomson, A., 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.

Alfaro, R., Campbell, R., Vera, P., Hawkes, B., Shore, T., 2004. Dendroecological reconstruction of mountain pine beetle outbreaks in the Chilcotin plateau of British Columbia. In: Shore, T.L., Brooks, J.E., Stone, J.E. (Eds.), Mountain Pine Beetle Symposium: Challenges and Solutions. Natural Resources Canada, Canadian Forest Service, Pac. For. Centre, Victoria, BC, Canada (Inf. Rep. BC-X-399).

Alfaro, R.I., Axelson, J., Lewis, K., Barichivich, J., Duran, L., Gee, H., Haavik, L, Hardy, K., Jones, E., Lopez, L., Mansilla, C., Pena, M., Suarez, L., 2008. Dendroecological reconstruction of western spruce budworm (*Choristoneura occidentalis* Freeman) at McCall Lakes, Peachland, British Columbia, Canada. North American Dendroecological Fieldweek. <http://dendrolab.indstate.edu/nadef/2008.htm> (accessed June 2014).

Alfaro, R.I., Berg, J., Axelson, J., 2014. Periodicity of western spruce budworm in Southern British Columbia, Canada. For. Ecol. Manage. 315, 75–79. http://dx.doi.org/10.1016/j.foreco.2013.12.026.

British Columbia Ministry of Forests, Lands and Natural Resource Operations., 2012. Facts about B.C.'s Mountain pine beetle. <http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/facts.htm (accessed March 2014).

British Columbia Ministry of Forests and Range., 1995. Defoliator Management Guidebook. <http://www.for.gov.bc.ca/tasb/legsregs/fpc/fpcguide/defoliat/defoltoc.htm> (accessed June 2014).

British Columbia Ministry of Forests and Range., 2007. Timber Supply and the Mountain Pine Beetle Infestation in British Columbia: 2007. <http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/Pine_Beetle_Update20070917.pdf> (accessed March 2014).

Boulanger, Y., Arseneault, D., Morin, H., Jardon, Y., Bertrand, P., Dagneau, C., 2012. Dendrochronological reconstruction of spruce budworm (*Choristoneura fumiferana*) outbreaks in southern Quebec for the last 400 years. Can. J. For. Res. 42 (7), 1264–1276. http://dx.doi.org/10.1139/x2012-069.

Bunn, A., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124.

Bunn, A., Korpela, M., Biondi, F., Campelo, F., Merian, P., Qeadan, F., Zang, C., 2012. dplR: Dendrochronology program library in R. package version 1.5.6. <http://www.cran.r-project.org/package=dplR> (accessed June 2014).

Burns, R., Honkala, B., 1990. Silvics of North America Volume 2 : Hardwoods. USDA For. Serv., Washington, DC, USA 2.

Campbell, R., Smith, D., Arsenault, A., 2005. Dendroentomological and forest management implications in the Interior Douglas-fir zone of British Columbia, Canada. Dendrochronologia 22, 135–140.

Campbell, R., Smith, D., Arsenault, A., 2006. Multicentury history of western spruce budworm outbreaks in interior Douglas-fir forests near Kamloops, British Columbia. Can. J. For. Res. 36, 1758–1769.

Chen, Z., Kolb, T., Clancy, K., 2001. Mechanisms of Douglas-fir resistance to western spruce budworm defoliation: bud burst phenology, photosynthetic compensation and growth rate. Tree Physiol. 21, 1159–1169.

Chen, P.-Y., Welsh, C., Hamann, A., 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. Glob. Change Biol. 16, 3374–3385. http://dx.doi.org/10.1111/j.1365-2486.2010.02166.x.

Clancy, K., 1992. Response of western spruce budworm (Lepidoptera: Tortricidae) to increased nitrogen in artificial diets. Environ. Entomol. 21, 331–344.

Cook, E., Kairiukstis, L. (Eds.), 1990. Methods of Dendrochronology: Applications in the Environmental Sciences. Springer.

Cook, E., Peters, K., 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-Ring Bull. 4, 45–53.

Cook, E., Krusic, P., Holmes, R., Peters, K., 2007. Program ARSTAN Version 41d. <http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software>.

Daniels, L., Watson, E., 2003. Climate-fire-vegetation interactions in the Cariboo forests: a dendroecological analysis. Forest Innovation and Investment Forest Research Program Report, Victoria, B.C..

Erikson, R., 1992. History of important forest insects in the Cariboo Forest Region 1913–1991. Canadian Forest Service, Pacific Forestry Centre, FIDS Report 92-14.

Fellin, D., Dewey, J., 1982. Western spruce budworm. Forest Insect & Disease Leaflet 53. USDA, Forest Service.

Flower, A., Gavin, D., Heyerdahl, E., Parsons, R., Cohn, G., 2014. Drought-triggered western spruce budworm outbreaks in the interior Pacific Northwest: a multi-century dendrochronological record. For. Ecol. Manage. 324, 16–27.

Fritts, H., 1976. Tree Rings and Climate. Academic Press, London.

Furniss, R., Carolin, V., 1977. Western Forest Insects. United States Department of Agriculture, Forest Service. Miscellaneous Publication No. 1339, Washington, DC.

Griesbauer, H., Green, D., 2010. Regional and ecological patterns in interior Douglas-fir climate–growth relationships in British Columbia, Canada. Can. J. For. Res. 40, 308–321.

Hadley, K., Veblen, T., 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. Can. J. For. Res. 23, 479–491.

Harris, J., Alfaro, R., Dawson, A., Brown, R., 1985. The Western Spruce Budworm in British Columbia 1909–1983. Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-257.

Holmes, R., 1986. Users manual for program COFECHA. In: Holmes, R.L., Adams, R.K., Fritts, H.C. (Eds.), Tree-Ring Chronologies of Western North America: California, Eastern Oregon and Northern Great Basin Ariz. Chronol. Ser. VI. University Of Arizona, Tucson, pp. 41–49.

Holmes, R., Swetnam, T., 1996. Program OUTBREAK Users Manual, Dendrochronology Program Library. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona.

Jardon, Y., Morin, H., 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.

Kozlowski, T., 1969. Tree physiology and forest pests. J. Forest. 67, 118–123.

Larocque, S., Smith, D., 2003. Little ice age activity in the Mt. Waddington area, British Columbia coast mountains, Canada. Can. J. Earth Sci. 40, 1413–1436.

Liebhold, A., Koenig, W., Bjørnstad, O., 2004. Spatial synchrony in population dynamics. Annu. Rev. Ecol. Evol. Syst. 35, 467–490.

Littell, J., Peterson, D., Tjoelker, M., 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. Ecol. Monogr. 78, 349–368. http://dx.doi.org/10.1890/07-0712.1.

Little, E. Jr., 1971. Atlas of United States Trees (Vol. 1): Conifers and important Hardwoods. U.S. Department of Agriculture, Miscellaneous Publication 1146.

Lo, Y.-H., Blanco, J., Seely, B., Welham, C., Kimmins, J., 2010. Relationships between climate and tree radial growth in interior British Columbia, Canada. For. Ecol. Manage. 259, 932–942. http://dx.doi.org/10.1016/j.foreco.2009.11.033.

Maclauchlan, L., Brooks, J., 2009. Influence of past forestry practices on western spruce budworm defoliation and associated impacts in southern British Columbia. BC J. Ecosyst. Manage. 10, 37–49.

Maclauchlan, L., Brooks, J., Hodge, J., 2006. Analysis of historic western spruce budworm defoliation in south central British Columbia. For. Ecol. Manage. 226, 351–356.

McLane, S., Daniels, L., Aitken, S., 2011. Climate impacts on lodgepole pine (*Pinus contorta*) radial growth in a provenance experiment. For. Ecol. Manage. 262, 115–123. http://dx.doi.org/10.1016/j.foreco.2011.03.007.

Meidinger, D., Pojar, J., 1991. Ecosystems of British Columbia. B.C. Min. For., Victoria, BC. Spec. Rep. Ser. 6.

Mekis, É., Vincent, L., 2011. An overview of the second generation adjusted daily precipitation dataset for trend analysis in Canada. Atmos. Ocean 49, 163–177.

Moran, P., 1953. The statistical analysis of the Canadian lynx cycle. Aust. J. Zool. 1, 291–298.

Murdock, T., Taylor, S., Flower, A., Mehlenbacher, A., Montenegro, A., Zwiers, F., Alfaro, R., Spittlehouse, D., 2012. Pest outbreak distribution and forest management impacts in a changing climate in British Columbia. Environ. Sci. Policy 26, 75–89. http://dx.doi.org/10.1016/j.envsci.2012.07.026.

Nealis, V., 2012. The phenological window for western spruce budworm: seasonal decline in resource quality. Agric. For. Entomol. 14, 340–347.

Nealis, V., Nault, J., 2005. Seasonal changes in foliar terpenes indicate suitability of Douglas-fir buds for western spruce budworm. J. Chem. Ecol. 31, 683–696.

Peltonen, M., Liebhold, A., Bjørnstad, O., Williams, D., 2002. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. Ecology 83, 3120–3129.

R Development Core Team., 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org/> (accessed June 2014).

Royama, T., 1984. Population dynamics of the spruce Budworm *Choristoneura fumiferana*. Ecol. Monogr. 54, 429–462.

Ryerson, D., Swetnam, T., Lynch, A., 2003. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, USA. Can. J. For. Res. 33, 1010–1028.

Shepherd, R., 1994. Management strategies for forest defoliators in British Columbia. For. Ecol. Manage. 68, 303–324.

Starheim, C., Smith, D., Prowse, T., 2012. Dendrohydroclimate reconstructions of July–August runoff for two nival-regime rivers in west central British Columbia. Hydrol. Process.. http://dx.doi.org/10.1002/hyp.

Steen, O., Coupé, R., 1997. A field guide to forest site identification and interpretation for the Cariboo Forest Region. Ministry of Forests, Research Program. <http://www.for.gov.bc.ca/hfd/pubs/docs/lmh/lmh39.htm> (Accessed May 2014).

Swetnam, T., Lynch, A., 1989. A tree-ring reconstruction of western spruce budworm history in the southern rocky mountains. For. Sci. 35, 962–986.

Swetnam, T., Lynch, A., 1993. Multicentury regional-scale patterns of western spruce budworm outbreaks'. Ecol. Monogr. 63, 399–424.

Swetnam, T., Wickman, B., Paul, H., Baisan, C., 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the Northern Blue Mountains, Oregon, since A.D. 1700. USDA Forest Service Research Paper PNW-RP-484.

Thomson, A., van Sickle, G., 1980. Estimation of tree growth losses caused by pest activity. Can. J. For. Res. 10, 176–182.

Torrence, C., Compo, G., 1998. A practical guide to wavelet analysis. Bull. Am. Meteorol. Soc. 79, 61–78.

van Sickle, G., Alfaro, R., Thomson, A., 1983. Douglas-fir height growth affected by western spruce budworm. Can. J. For. Res. 13, 445–450.

Vincent, L., Wang, X., Milewska, E., Wan, H., Yang, F., Swail, V., 2012. A second generation of homogenized Canadian monthly surface air temperature for climate trend analysis. J. Geophys. Res. 117, D18110. http://dx.doi.org/10.1029/2012JD017859.

Wang, T., Hamann, A., Spittlehouse, D., Murdock, T., 2012. ClimateWNA—high-resolution spatial climate data for western North America. J. Appl. Meteorol. Climatol. 51, 16–29. http://dx.doi.org/10.1175/JAMC-D-11-043.1.

Watson, E., Luckman, B., 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. http://dx.doi.org/10.1139/X02-096.

Watson, E., Luckman, B., 2004. Tree-ring based reconstructions of precipitation for the southern Canadian Cordillera. Climatic Change 65 (1–2), 209–241.

Westfall, J., Ebata, T., 2000–2011. Summary of forest health conditions in British Columbia. Pest Management Report Number 15. Forest Practices Branch, Victoria, BC. <http://www.for.gov.bc.ca/hfp/health/overview/overview.htm> (accessed May 2014).

Williams, D., Liebhold, A., 2000. Spatial synchrony of spruce budworm outbreaks in eastern North America. Ecology 81, 2753–2766.

Woods, A.J., Heppner, D., Kope, H., Burleigh, J., Maclauchlan, L., 2010. Forest health and climate change: a British Columbia perspective. Forest. Chron. 86, 412–422.

Yamaguchi, D., 1991. A simple method for cross-dating increment cores from living trees. Can. J. For. Res. 21, 414–416.

Zang, C., 2012. bootRes: bootstrapped response and correlation funcitons. R package version 1.2.3. <http://www.cran.r-project.org/web/packages/bootRes/index.html>.

Zang, C., Biondi, F., 2012. Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. Dendrochronologia 31, 68–74.