Identifying Western Spruce Budworm Defoliation Events in the IDF Zone using Dendroentomology

Ву

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Abstract

A dendroentomological analysis has been conducted for one site in the Interior Douglas-fir biogeoclimatic zone in near Clinton, British Columbia, Canada. This is a pilot study of work that is to be part of a synthesis of data collected from 30 throughout the southern interior forests of British Columbia. The study aims to reconstruct defoliation events caused by western spruce budworm (Choristoneura occidentalis Freeman) on the host species Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco). Defoliation from western spruce budworm causes a reduction in tree radial growth and can be visually identified in the tree rings. This paper discusses western spruce budworm biology, history in British Columbia, and implications that climate change may have on the future ecologic integrity of the study area and on future outbreaks. As a test of analytical methods, western spruce budworm defoliation history was studied by identifying periods of reduced growth using cores taken from 20 Douglas-fir trees from one site in an area of known defoliation near Clinton, British Columbia. Dendrochronological software CooRecorder and CDendro were used to measure tree ring widths and crossdate the data, respectively. The Douglas-fir host chronology was compared to a non-host ponderosa pine (Pinus ponderosa Douglas ex C. Lawson) chronology to account for any climatic variations that may also cause growth reductions. This study resulted in the identification of eight distinct suppression events from 1685 to 1965 that were likely caused by the western spruce budworm in the Clinton region.

Keywords

Defoliation, dendrochronology, dendroentomology, western spruce budworm, climate change, natural disturbance

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Introduction

Reasons for Conducting Research

Dendroentomological methods have been used to reconstruct historical defoliations of western spruce budworm (Choristoneura occidentalis Freeman) in the interior of British Columbia (Campbell, Smith, & Arsenault, 2005;2006). Knowledge of forest disturbance history of the interior Douglas-fir (IDF) biogeoclimatic (BEC) zone is essential for understanding the impacts defoliating insects have on forest productivity in the short and long terms. Western spruce budworm is a native defoliator that has the potential to have large-scale impacts and when it periodically reaches outbreak levels in British Columbia. Biotic disturbances can be damaging to the health of the forest, but they are also an integral component of a healthy ecosystem. Biotic disturbances are important drives of forest dynamics and are described by disturbance regime attributes: a spatial disturbance pattern, frequency and magnitude (intensity and severity) of disturbances, and a resulting ecological pattern over space and time (Pickett & White, 1985; Menendez & Stone, 2009). The action of biotic disturbance aids the forest to naturally renew itself, increase biodiversity through habitat creation, and increase nutrient cycling and availability (Ryerson, Swetnam, & Lynch, 2003). However, large outbreaks can cause disturbances to surpass the allowable threshold, the ecological pinch point, of the ecosystem. The resulting forest insects become pests that threaten the environmental integrity of the forest, reduce forest productivity, and control forest dynamics (Pickett & White, 1985).

Disturbance history is an important aspect for forest resource management since a better understanding of forest ecosystems and past events permits forest modellers to predict more accurate changes of forest and stand level disturbances in response to climate change (Fritts & Swetnam, 1989; Swetnam et al. 1999). Climate change has the potential to affect forests by shifting the magnitude, frequency, timing and duration of biotic disturbances. It may also influence introduced insect species to the ecosystem that can further alter the disturbance regime in a negative way (Gayton, 2008). Climate change is projected to impact disturbance dynamics due to an overall higher average temperature and varying precipitation patterns.

Direct effects on insect species include changes to their development, abundance, and geographical range. Temperature increases will effect exothermic species fertility and mortality as well as accelerate their development rates (reduced duration of life-cycles) including voltinism and diapause (Netherer, 2009) and extended periods of warm and dry weather in British Columbia could increase the density of budworm populations (Campbell, 1989). Climate could also be important in beginning synchrony between larval emergence and bud break (Campbell, Smith, & Arsenault, 2005). Changing patterns of precipitation from climate change will affect tree vigour and resistance to disease and insects, plant water cycles, and tree growth-rate (Johnston et al., 2010). In fact, it has been reported in south-central Colorado that western spruce budworm outbreaks correspond to times of increased moisture (Ryerson, Swetnam, & Lynch, 2003).

The future disturbance and insect disturbance regimes will also be affected by climate change through impacts on the ecology of natural enemies and diseases (European Forest Institute, 2008). Invasive forest insects such as the emerald ash borer (*Agrilus planipennis*) and the Asian stink bug (*Halyomorpha halys*) have grown in population sizes in the United States are threatening the existence of ash trees and fruit crop productivity respectively in high infestation areas (Fawcett, 2012). Impacts from the mountain pine beetle (*Dendroctonus ponderosae*), a native insect in in British Columbia, include massive tree mortality and timber losses throughout the province and an expansion of its range into Alberta (Carroll et al., 2006). As for the western spruce budworm, because of its broad geographic range and impacts on timber resources, it is considered to be one of the most destructive insects on timber production in western coniferous forests (Fellin & Dewey, 1986).

Biology and History of the Western Spruce Budworm

Defoliators are insects that feed on the leaves and needles of trees (British Columbia Ministry of Forests, 2000). General symptoms of damage include discoloration or loss of foliage, damaged needles and leaves that have been eaten or chewed that may be on the tree or the ground, and the presence of frass. Overall effects of western spruce budworm infestation include reddish brown foliage and chewed needles accumulated in webbing at branch tips, top

kill, reduced radial and height growth as well as stem deformities, and, rarely, tree death (Kramer & Kazlowski, 1979). Western spruce budworm destroys photosynthetic tissue, reduces radial growth, and reduces apical growth during each year of defoliation. Forest insect defoliators are classified by the structures that they use and produce while feeding; examples include leafrollers and leafeaters, webworms and casebearers, and some insects consume leaves but do not make a structure. Other defoliators in interior British Columbia include the western hemlock looper (*Lambdina fiscellaria lugubrosa*), eastern spruce budworm (*Choristoneura fumiferana*), Douglas-fir tussock moth (*Orgyia pseudotsugata*), and the western blackheaded budworm (*Acleris gloverana*); the latter two can also affect Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) trees.

The western spruce budworm was first recorded in 1909 on Vancouver Island and infestations have been recorded throughout British Columbia ever since (B.C. Ministry of Forests, Land and Natural Resource Operations, 2012). It commonly affects Douglas-fir forests in the interior but also feeds upon true firs, larch and spruce trees of all ages, although mature trees are more vulnerable. Over the last century, outbreak frequency, length and severity may have increased as a result of forest management practices such as fire exclusion, selected harvesting of ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) trees leaving a greater Douglas-fir component, in addition to changing temperature and precipitation patterns. Specifically, severe historical western spruce budworm infestations may be a function of warm dry summers, at the stage in which optimal synchrony between larval emergence and bud flush increases susceptibility of Douglas-fir trees to be attacked (Thomson, Shepherd, Harris, & Silversides, 1984).

In 1987 and 2007-2008, over 800 000 hectares in southern interior BC were affected by western spruce budworm (B.C. Ministry of Forests, Land and Natural Resource Operations, 2012). When populations reach very high densities, larvae will consume all new foliage then back-feed on the older foliage causing substantial damage in one growing season (B.C. Ministry of Forests, 1995). Outbreaks of high severity are the result of improved reproduction and survival rates of the insects or spread from neighbouring locations also infested (Campbell, 1993). Typically,

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defoliation occurs in elevational bands across mountain sides, especially on south and westfacing slopes and reoccurs in the same general site during subsequent outbreaks (Heppner & Turner, 2006). On average, outbreaks last three to five years and sometimes upwards of ten or more.

Defoliation events that continue over a number of years can cause mortality in the upper crown and reduces the height of the trees in the overstorey by one to several internodes (Alfaro & MacLauchlan, 1992). Stand dynamic factors such as stand density, height structure, vigor, maturity, size and climate govern the susceptibility of Douglas-fir to western spruce budworm (Torgersen 2001; Carlson 1988). Once defoliation has occurred, defoliated trees require several years to recover their full foliage (Campbell, Smith, & Arsenault, 2005). Essentially, the effect of defoliation is governed by the host species and the insect, the frequency and timing of feeding, and the overall physiological condition of the tree (Alfaro & MacLauchlan, 1992).

Dendrochronology and Stem Analysis

Disturbances such as fire, insect attack, climate variations and other disturbances are visually evident in conifer tree-ring series as variation or anomalies in the width of annual growth rings (Campbell, Smith, & Arsenault, 2005). Therefore, the disturbance history of a stand is recorded over time in the rings of individual trees that can be analysed using dendrochronological methods and compiled for multiple trees to quantify the magnitude and severity of individual disturbance events.

Dendrochronology is a method of tree-dating based on analysing tree ring growth and patterns. Essentially, it is the study of growth rings over time. It is based on seven principles (Grissino-Mayer, 2010):

 The Uniformitarian Principle: Tree rings can be used to infer past environmental conditions if the physical and biological processes linking current environmental processes with current patterns of tree growth were also present in the past. This is often described as "the present is the key to the past."

- The Principle of Limiting Factors: The rates of plant processes can only occur as fast as that which is allowed by the factor that is most limiting.
- The Principle of Aggregate Tree Growth: Variation in any individual tree-growth series can be explained by an aggregate of environmental factors, natural and human caused, that affect the patterns of tree growth over time. Aggregate factors include tree age, climate, disturbance factors within and from outside the forest stand and random error.
- The Principle of Ecological Amplitude: Species can grow, reproduce, and proliferate across wide or narrow ranges of habitat. Tree species useful for dendrochronological analyses of climate variation are often found near the margins of their natural range.
- The Principle of Site Selection: Sites useful for dendrochronology should be based on criteria that generate tree-ring series sensitive to the environmental variable being studied.
- The Principle of Crossdating: Matching patterns in ring widths and other ring characteristics, such as density patterns, amongst tree-ring series from multiple trees allows the identification of the exact calendar year in which the tree ring was formed. This type of pattern matching helps identify false or missing rings within a series and ensures accurate dating.
- The Principle of Replication: The environmental signal being studied that can be exploited, by examining more than one stem radius per tree, and more than one tree per site.

Dendroentomology is the science of using tree rings to date and study the past dynamics of insect populations. Tree-ring series can be used to reconstruct past insect defoliator outbreaks because defoliations leave a distinct signature in the width of tree rings. Recognized periods of low or reduced growth have been observed in Douglas-fir trees and the respective years of the outbreak can be traced through time. During successive years of infestation, the width of the annual growth rings is reduced, an effect that produces a relationship that has a one or more year lag (Alfaro & MacLauchlan, 1992).

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Objective

The purpose of this study is to reconstruct western spruce budworm defoliation history of Douglas-fir trees at one site in the Interior Douglas-fir (IDF) zone, to compare suppression events among trees within a site to detect outbreaks, and to catalogue outbreak(s) duration, frequency and severity. By comparing the ring-widths of Douglas-fir with a non-host species ponderosa pine, it is anticipated that I can detect the effects of defoliation by western spruce budworm on the Douglas-fir trees in the IDF zone generated from possible climate change by reconstructing outbreaks and interpreting if the disturbance regime is changing over time.

Study Area

The study area (figure 1) is located at UTM 10, N51°06′53.5″ and W121°34′18.9″, approximately three kilometres northeast of Clinton, British Columbia in the IDF biogeoclimatic zone. The IDF biogeoclimatic zone (IDF) is comprised of mid- to low-elevation (300m - 1450m) forests throughout the southern and central British Columbia, and generally occurs below the Montane Spruce zone and above the Ponderosa Pine zone. Northern areas of the IDF zone are surrounded by the Sub-boreal Pine – Spruce and Sub-boreal spruce zones, as well as the Bunchgrass zone. Combined, these zones occupy the majority of the southern part of the Interior Plateau. The Coast and Cascade mountain ranges generate a rain-shadow over the IDF zone, creating a warm and dry summer season and a cool winter. Annual rainfall ranges from 295 – 750mm and mean annual temperatures vary between 1.6 - 9.5°C (Lloyd et. al., 1990). The growing season is vulnerable to moisture deficits and frosts can occur frequently, at any time of year. The ecology of the area is a product of the shortage of moisture in much of the zone and effective precipitation is directly governed by evaporation rates via temperature.

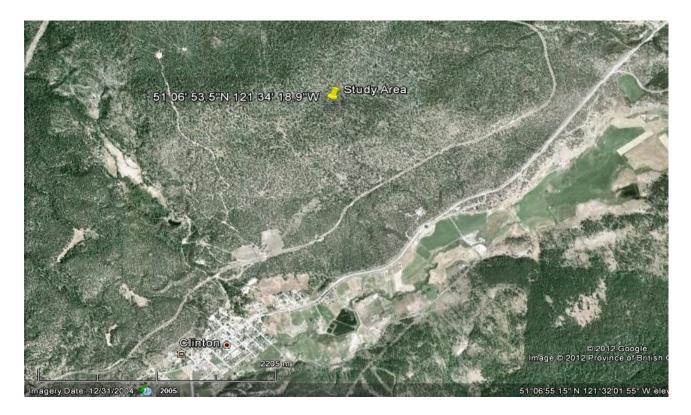


Figure 1. Map of site location showing location of Douglas-fir stands sampled in the study (Source: Google EARTH).

Methods

The host stand was selected from an area of known defoliation in the Southern Interior Forest Region, near Clinton. This study is a part of a larger project that will include analysis of 800 increment cores taken from 35 sites. For this paper, 20 Douglas-fir (host species) were selectively cored at approximately 1.3 metres above the point of germination from one site. In the laboratory, each increment core was mounted on blocks and sanded with 320 and 400 grit sandpaper using a belt-sander (Stokes & Smiley, 1968). Each core was scanned with an EPSON printer, set to 16-bit grayscale and 2400 dots per inch, resulting in a TIF image, which was then converted into GIF format such that it could be processed to generate crossdated ring-width series. Measuring and crossdating of the cores were completed using digital software Cybis Coordinate Recorder (CooRecorder) and CDendro respectively (Larsson, 2011). When needed, the ring-width measurements were verified by visually checking the rings using a stereo-zoom microscope. Output files (.pos) from CooRecorder were analyzed in CDendro and outer rings of 2011 were assigned to each core, assuming the tree was alive and had formed a complete ring

at the time they were cored in late summer or early fall 2011. The oldest sample (327 years old) was used as the reference samples for crossdating all other series. Following this preliminary step, output files from CDendro were cross-dated against an existing Douglas-fir chronology (Daniels & Watson, 2003) for quality control using the software COFECHA, from the International Tree Ring Data Bank (Grissino-Mayer, 2001). COFECHA utilizes segmented time-series in order to assess the quality of crossdating in a measurement series (Grissino-Mayer, 2010) as well as to detect errors and outlier ring measurements (Grissino-Mayer, 2001). Correlations of 50-year segments, lagged by 25 years, were used.

Segments with low correlations or that indicated possible errors due to missing rings were checked and corrected using CooRecorder and CDendro until all rings were properly dated and a significant correlation was achieved for each series.

Once crossdated, the ring-width series were combined into a master ring-width series using the program COFECHA and summary statistics for the original ring-width measurements and filtered data were derived. In COFECHA, a 32-year spline function acting like a "window" of years is used to calculate a moving average for each ring-width series (Grissino-Mayer, 2001). A shorter window or spline length may misinterpret the data by eliminating too many of the ecological signs that contribute to the development of tree-rings. The 32-year spline function is used to de-trend each tree-ring series and allow COFECHA's autoregressive modelling to remove the autocorrelation for each series. The autocorrelation value specifies the degree of association between subsequent values within each chronology time series. For the filtered data, all of the series have been standardized to 0.0.

The program OUTBREAK, version 6.00P, was used to identify signature outbreaks that met the user-defined criteria for western spruce budworm. Within the program, two analyses are conducted. First, each crossdated Douglas-fir ring-width series was standardized against a chronology from a non-host species, ponderosa pine, to account for climatic variation that would cause narrow rings or periods of suppression with the measured ring series. The ponderosa pine chronology was acquired from the Tree Ring Data Bank (Fritts, 1965). This chronology was developed from trees growing near Kamloops in the IDF. The control

chronology dates from 1590 to 1965 and had a mean sensitivity of 0.321 and a standard deviation of 0.380.

In the second step, the program OUTBREAK applies a set of user-defined criteria for identifying growth reductions likely due to an insect outbreak. For this analysis, growth reductions that were at least 1.28 standard deviations below the mean and the minimum number of years for a recognized outbreak was set at eight (Campbell, Smith, & Arsenault, 2005). Western spruce budworm outbreaks were omitted by the program OUTBREAK if it did not attain at least eight years at the end of the series.

At the tree-level, all suppressions were identified and summary statistics were compiled that include the percent of growth reduction for all suppressions and the year when the maximum percentage of growth reduction occurred. At the stand-level, the total number of suppressed trees were determined for each year as well as the proportion of living trees determined to be suppressed according to the criteria defined in OUTBREAK; these results were presented in frequency distributions. Two criteria were defined for modes: peaks greater than 50% prior 1900, when the number of living trees was less than or equal to 12, and peaks greater than 10% after 1900, when number of living trees was between 13 and 20. Outbreaks of western spruce budworm most likely occur in modal years.

Results

The master series for the site near Clinton contains 20 Douglas-fir trees with the oldest tree dating back 327 years (Table 1). The mean series intercorrelation was 0.785 and average mean sensitivity was 0.324. This high series intercorrelation value indicates a strong signal common to all sampled trees from the site (Fritts, 1976; Grissino-Mayer, 2001); it indicates the chronology is very consistent and reliable. Mean sensitivity is the relative change in ring-widths from one year to the next for the series and may strongly vary depending on species and regional climate (NCDC, 2008). The average mean sensitivity of 0.324 indicates that the Douglas-fir host species is somewhere in-between complacent and sensitive tree growth reaction to regional climate characteristics.

Table 1. Summary statistics derived using the program COFECHA for the Douglas-fir ring-width chronology for the study site near Clinton, BC.

Summary Data	
Number of Dated Series	20
Master Series (1685 - 2011)	327 years
Total Rings in all Series	2936
Total Dated Rings Checked	2829
Series Intercorelation	0.785
Average Mean Sensitivity	0.324
Segments, Possibly Problems (Flags)	0

Douglas-fir trees at the study site average 147 years old and most were less than 200 years old, but the oldest core from the study site was found to be 327 years old (Table 1 and Figure 2) and visually exhibited periods of reduced growth in the tree rings (Figure 3). The reduced growth is evident in the narrow ring and reduced production of earlywood and latewood. Through the OUTBREAK software, it was determined that this particular period of reduced growth met the criteria that identify growth suppressions caused by the western spruce budworm (Figure 3).

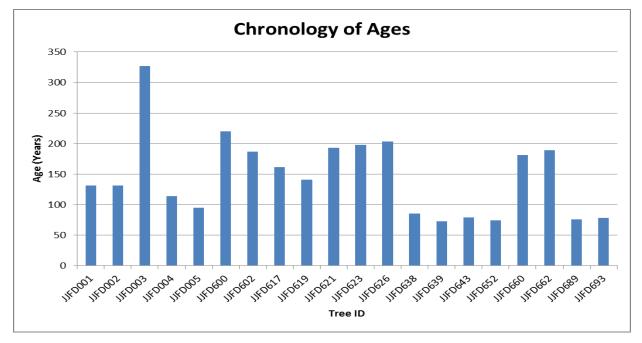


Figure 2, Chronology of Tree Ages for 20 Douglas-fir host trees at the study site near Clinton, BC.

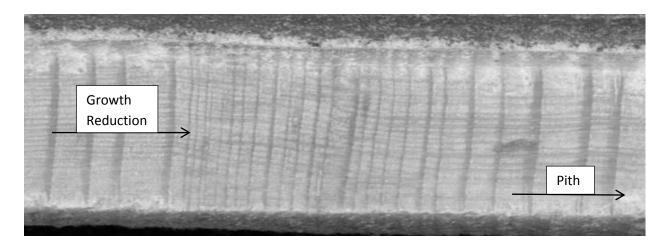


Figure 3. Increment core from sample JJFD003 with pronounced reductions of growth (reduction >1.28 standard deviations below the mean and sustained >8 years) likely due to defoliation by western spruce budworm. Increased growth was evident by the larger growth rings following the defoliation event.

The COFECHA output, including descriptive statistics for the master series, as well as the unfiltered and filtered data for the individual ring-width series are compiled in Table 3. High values, 0.30 or greater, have resulted for the mean series sensitivity of the unfiltered data for individual ring-width series (Table 3). The average values for mean sensitivity for the unfiltered data measured 0.324 and the average standard deviation was 0.039. The auto-correction values for the filtered data all measured close to zero, indicating that filtering effectively removed the autocorrection and the measurements were relatively persistent one year to the next. The average correlation corresponding to the master chronology is an important statistic for interpreting the strength of the cross-dating for the site and values higher than 0.50 are desirable. The correlation with the master chronology ranged from 0.706 to 0.865 with an average of 0.785, indicating a strong correlation for the sample site. There were zero flags associated with individual trees within the crossdated host species chronology indicating all 50-year segments of all trees was properly dated and highly correlated with all other trees.

Fourteen of 20 trees included suppressions that met the minimum criteria for western spruce budworm detection from OUTBREAK. Eight trees from the sample site were calculated to be supressed more than once. In total, 25 outbreak suppressions were recorded with the majority of the maximum growth reduction years occurring in the 1800s and early 1900s. The average length of outbreak was 15 years, however, outbreaks ranged from 8 to 42 years in length, with

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three exceeding 21 years. The average magnitude of the 25 growth reductions was 2.81% and ranged from 0.87% to 6.58%. The maximum growth reduction for the experimental chronologies ranges from 3.54 to 13.36%; the average maximum growth reduction was 7.64% for the site. However, OUTBREAK calculated the length of growth suppressions to exceed 21 years for three samples (JJFD003, JJFD602 and JJFD626 in Table 3), indicating that reduced growth due to defoliation and infestation combined with possible poor regional climate conditions can be detrimental to overall tree-ring growth and forest productivity for decades.

Considering all 25 suppressions between 1685 and 1965, the period corresponding to the oldest Douglas-fir ring-width series and end of the control ponderosa pine chronology, five distinct periods when many trees were supressed, likely due to a western spruce budworm outbreak, were identified using the program OUTBREAK (Figure 4). However, the period from 1807 to 1885, there appeared to be four different events (Table 4), making the total number of identified outbreaks eight.

The degree of growth reduction per maximum outbreak year varies considerable through the time scale of this study (Figure 5). The average reduction of growth was proportional to the length of the outbreak. For instance, between 1801 and 1842 there was maximum growth reduction of 13%. The proportion of infested trees was greatest between 1828 and 1838 (Figure 5) when six out of eight trees in the sample site were supressed. Both the number and proportion of supressed trees has declined since the 1870s, with less than 20% of the sample trees showing significant signs of suppression during possible outbreaks after 1900 (Figures 4 and 5). The overall proportion of supressed trees was lower (Figure 5) and growth reductions in the 1900s were relatively low compared to suppression events of the 1800s (Figure 6). The periods of these outbreaks were shorter than suppression outbreaks in the 1800s.

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Table 2. Descriptive statistics derived using the program COFECHA for individual ring-width series from host Douglas-fir trees growing near Clinton, BC.

	50 Year Segments (lagged 25 years)	No. Flags	Correlation to Master	Unfiltered Data				Filtered Data			
Interval				Mean Measurement	Max Measurment	Standard Deviation	Auto- correlation	Mean Sensitivity	Max Value	Standard Deviation	Auto-Correlation
1881 - 2011	5	0	0.852	0.09	0.25	0.040	0.652	0.300	2.55	0.426	-0.025
1881 - 2011	5	0	0.785	0.09	0.22	0.042	0.689	0.276	2.68	0.406	-0.023
1685 - 2011	9	0	0.710	0.05	0.26	0.037	0.776	0.358	2.64	0.337	-0.024
1898 - 2011	5	0	0.780	0.07	0.21	0.043	0.739	0.315	2.72	0.447	-0.113
1917 - 2011	4	0	0.760	0.12	0.29	0.063	0.808	0.269	2.72	0.467	-0.035
1792 - 2011	9	0	0.773	0.06	0.19	0.031	0.620	0.322	2.79	0.446	-0.008
1825 - 2011	7	0	0.763	0.09	0.26	0.047	0.652	0.310	3.04	0.436	-0.042
1851 - 2011	6	0	0.832	0.06	0.14	0.026	0.625	0.296	2.57	0.429	-0.031
1871 - 2011	6	0	0.861	0.08	0.22	0.035	0.621	0.333	2.77	0.463	0.016
1819 - 2011	8	0	0.778	0.04	0.10	0.020	0.600	0.374	2.60	0.365	-0.012
1814 - 2011	8	0	0.750	0.07	0.24	0.044	0.696	0.325	2.92	0.397	-0.064
1809 - 2011	8	0	0.706	0.07	0.24	0.041	0.649	0.326	2.93	0.448	-0.041
1927 - 2011	3	0	0.792	0.12	0.33	0.072	0.723	0.334	2.79	0.452	-0.084
1939 - 2011	3	0	0.865	0.10	0.22	0.049	0.749	0.261	2.76	0.554	0.031
1933 - 2011	3	0	0.781	0.09	0.24	0.056	0.823	0.275	2.79	0.475	-0.016
1938 - 2011	3	0	0.777	0.09	0.20	0.046	0.738	0.312	2.72	0.401	0.024
1828 - 2011	7	0	0.863	0.05	0.15	0.026	0.583	0.374	2.54	0.382	0.003
1823 - 2011	8	0	0.802	0.05	0.15	0.029	0.651	0.334	2.65	0.414	-0.030
1936 - 2011	3	0	0.751	0.09	0.24	0.051	0.746	0.319	2.90	0.561	0.014
1934 - 2011	3	0	0.828	0.10	0.25	0.057	0.786	0.313	2.92	0.536	-0.078
	113	0	0.785	0.07	0.33	0.039	0.683	0.324	3.04	0.425	-0.027

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using			the		program		OUTBREAK.
Tree ID	Inner Most Ring (Year)	Outer Most Ring (Year)	Outbreak Timespan (>8 years min.)	Length of Outbreak (Years)	Average Growth Reduction (%)	Maximum Growth Reduction (Year)	Maximum Growth Reduction (%)
JJFD001	1881	1965	1881 - 1888	8	4.10	1881	11.02
JJFD002	1881	1965	1942 - 1949	8	2.29	1946	8.33
JJFD003			1686 - 1693	8	2.41	1692	6.97
11-002	1685	1965	1801 - 1842	42	5.06	1832	13.36
			1942 - 1952	11	3.03	1946	11.08
JJFD004	1898	1965	1955 - 1965	11	3.05	1962	8.81
JJFD005	1917	1965	none	0	none	none	none
			1807 - 1816	10	3.20	1814	9.43
JJFD600			1908 - 1918	11	0.87	1913	3.54
	1792	1965	1942 - 1949	8	1.75	1946	6.48
JJFD602	1825	1965	1825 - 1863	39	6.58	1832	18.30
JJFD617	1851	1965	1865 - 1885	21	3.13	1884	6.07
JJFD619	1871	1965	1871 - 1890	20	4.81	1881	10.26
			1828 - 1842	15	1.83	1831	4.39
JJFD621	1819	1965	1846 - 1854	9	0.92	1853	4.01
			1828 - 1838	11	3.06	1829	6.29
JJFD623	1814	1965	1865 - 1877	13	2.67	1873	7.61
			1827 - 1863	37	3.95	1832	10.15
JJFD626	1809	1965	1870 - 1885	16	3.71	1883	6.47
JJFD638	1927	1965	none	0	none	none	none
JJFD639	1939	1965	none	0	none	none	none
JJFD643	1933	1965	none	0	none	none	none
JJFD652	1938	1965	none	0	none	none	none
			1828 - 1842	15	2.44	1831	5.90
JJFD660			1862 - 1873	12	1.62	1871	3.8
	1828	1965	1900 - 1916	17	2.07	1904	6.54
			1846 - 1862	17	2.11	1853	6.14
JJFD662			1907 - 1915	9	1.26	1913	3.66
	1823	1965	1934 - 1942	9	1.55	1939	4.75
JJFD689	1936	1965	1955 - 1963	9	2.79	1955	7.52
JJFD693	1934	1965	none	0	none	none	none
Mean				15	2.81		7.64

Table 3. Summary Statistics for suppressions in 20 individual Douglas-fir trees that met the criteria to be considered the result of defoliation by western spruce budworm

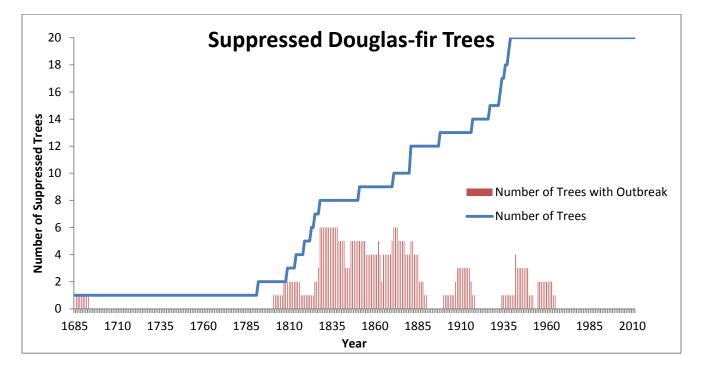


Figure 4. Number of Douglas-fir host trees alive (blue line) and supressed (red bars) from 1685 to 2011. Supressed trees meet the minimum criteria for detecting defoliations by western spruce budworm using OUTBREAK software.

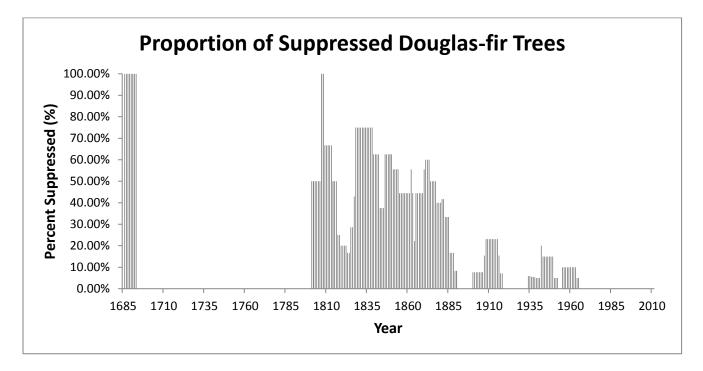


Figure 5. Proportion of infested Douglas-fir host trees suppressed from 1685 to 2011. Supressed trees meet the minimum criteria for detecting defoliations by western spruce budworm using OUTBREAK software.

Table 4. Detailed suppressions calculated in Douglas-fir host species from 1800 to 1885 that meet the minimum criteria for detecting defoliations by western spruce budworm using OUTBREAK software.

Outbreak	Length of	Average Growth	Max Growth	Max Growth
Timespan	Suppression	Reduction	Reduction	Reduction
	(Years)	(%)	(Year)	(%)
1807 - 1815	9	4.69	1814	9.24
1826 - 1489	17	4.57	1831	9.32
1849 - 1862	14	2.93	1583	6.47
1877 - 1885	9	3.15	1884	5.42

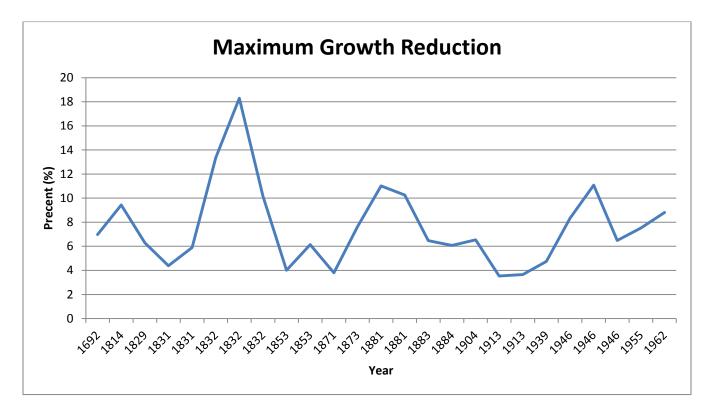


Figure 6. Maximum growth reductions possible due to outbreaks of western spruce budworm for the study period from 1686 to 1965.

Discussion

Result Implications

The analysis of growth suppressions in host Douglas-fir trees resulted in the detection of eight potential outbreaks of western spruce budworm in the Clinton area in British Columbia over the 281 years between 1685 and 1965. Tree growth and the resulting suppressed ring-widths will

differ depending on the regional and local climate, geographical area, tree species, site homogeneity, degree of on-site disturbance and stand competition (Grissino-Mayer H., 2001). This is important to note because over time each individual tree will go through independent stresses caused by limiting resources occurring at the microsite-scale. Stresses such as competition with other trees for light, moisture, and root access to below-ground resources may all play intricate roles in defining tree-ring growth patterns and can confound detections of past outbreaks. Detecting past outbreaks can be complicated because the tree ring response to defoliation can often be lagged by one to several years behind the initial defoliation event (Alfaro, Van-Sickle, Thomson, & Wegwitz, 1982). Some of these limitations were overcome in this study by using Douglas-fir and ponderosa pine chronologies. By comparing the two species, it has been demonstrated that western spruce budworm outbreaks have occurred periodically throughout the 375+ year tree ring record database constructed for Kamloops and the surrounding area. The comparison of the host Douglas-fir ring-width series to the non-host ponderosa pine was useful when studying patterns possibly due to the western spruce budworm outbreaks because they provide interpretations of past outbreaks while controlling for potential growth suppressions due to climatic variation (Swetnam & Lynch, 1993). Replication was also important for this study. By assessing many host trees, several periods can be identified when multiple trees were supressed which is more likely attributed to stand-level outbreak rather than a spurious result because of a growth irregularity in a tree caused by something other than western spruce budworm.

Health of the Stand and Ecosystem

The overall health of the forest will be dependent on more variables than just infestation of western spruce budworm; however forest health may govern successful western spruce budworm infestation. Forest characteristics such as nutritive value of the foliage could be a factor for budworm success in addition to synchrony and climatic influence (Campbell, Smith, & Arsenault, 2005). For this study, it was found that the average length of outbreak was roughly 15 years. As well, trees can take years to decades to recover, depending on the magnitude of the defoliation and damage to tree tissues. Nonetheless, the perseverance of the Douglas-fir in the study stand shows that the mature trees, even those defoliated multiple times, eventually

recover from outbreaks and can coexist with the western spruce budworm for long periods of time.

During a study of the western spruce budworm in the interior of British Columbia, Campbell et al (2005) found that the historical outbreak record in association with the local climate data suggested that the onset of an early spring and low accumulations of precipitation during winter months increased the success of western spruce budworm emergence. With the onset of climate change, warmer temperatures earlier in the season and changing precipitation patterns for the Clinton region, it can be predicted that Douglas-firs ability to defend against western spruce budworm foraging will decline. Furthermore, with higher overwintering survival coupled with increased budworm population growth and an altered growing season with possible reduced growing season moisture availability, outbreaks could expand in latitudinal range. Maclaughlan et al. (2006) found that trees in dry and stressed areas appear to be the most vulnerable to western spruce budworm. Hence, the outcome of climate change could alter the geographical range for western spruce budworm, while also increasing the number of available host Douglas-fir trees. This has important implications due to the arising pattern of lag between climatic variances and insect outbreaks, meaning that after a certain level of insect population density, the dynamics of the western spruce budworm outbreak could become less dependent on biophysical factors and increasingly related to population dynamics (Montenegro, 2008). As trees become maladapted to changing climate conditions, the hostspecies relationship for pathogens can change, and insect outbreaks could increase in frequency (Utzig & Holt, 2009) causing amplified Douglas-fir infestation rates and mortality.

Douglas-fir may become an increasingly important species in British Columbia due to the massive losses of pine species from the mountain pine beetle. Increased protection of Douglas-fir trees from spruce budworm may be required in order to protect the future health of the regional stands and ecosystem (Nealis, 2010). Furthermore, non-timber values may also be at risk due to the essential role Douglas-fir plays in regards to ecosystem hydrology and wildlife within the IDF zone.

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Uncertainties, Limitations and Recommendations for Improvement

To build on this pilot study of methods for reconstructing western spruce budworm outbreaks in British Columbia, it would be ideal for additional tree-ring chronologies to be completed and available for cross-dating within the IDF zone of British Columbia. The ponderosa pine control chronology from the International Tree Ring Databank ended in 1965, preventing analysis over the last 40 years. It is recommended that newer chronologies for non-host control species be developed in order to combine them with existing chronologies for the longest and most robust control. In addition, it may be beneficial to perform direct testing of climate-growth relations between Douglas-fir and ponderosa pine at the study site. Additional studies would be helpful in regards to tracking fine-scale suppressions that will help model for western spruce budworm infestations in response to climate change.

Using tree-ring chronologies as a method for measuring biotic disturbances was demonstrated in this study. There are other methods of measuring biotic disturbances such as Forest Insect and Disease Surveys (FIDS) which can be used to corroborate the tree-ring analyses. These aerial surveys are useful in reporting the general trend in defoliation patterns across large landbases and reporting summarizing health conditions of the forest. However, these surveys are limited in the manner that they likely do not detect fine-scale or mid-scale infestations. Also, records are limited as aerial surveys have only been recorded since 1911 by the British Columbia Ministry of Forests (BC Ministry of Forests, Lands and Natural Resoruce Operations, 2012).

Uncertainties inherently exist within the data because tree ring growth is a function of several environmental influences that include age trends and climate variations in addition to other disturbances (Ryerson, Swetnam, & Lynch, 2003). The study by Ryerson et al. (2003) also discusses that the growth reduction of surviving trees has the ability to provide a good indication of outbreak intensity but is constrained by the issue that surviving trees will not show the highest degree of growth reduction that results from an outbreak. Instead, trees that are impacted the most result in the death of the tree and the impact is lost from the tree-ring record. Thus, the results are strictly for affected and surviving trees, not the entire stand. Also,

the detected growth reductions are based on the user-defined criteria in the OUTBREAK software. Measurements of magnitude of the growth reductions may exist within the user-defined eight year window in the software OUTBREAK. Should the window be shortened, it is possible that there would be more suppression events measured. Conversely, if the window is widened to a longer timeframe, fewer suppression events would be measured. Forest management factors including silviculture systems and logging treatments must also be taken into consideration to ensure their respective impacts on tree-ring growth have not been reported as an insect outbreak in error.

Further research may be required to test the validity and reliability of the non-host species correction approach when reconstructing historical western spruce budworm and other insect outbreaks. Ryerson, Swetnam, and Lynch (2003) recommend supplementary research involving direct comparisons and experiments of insect populations and defoliation time series with tree ring time series. A sensitivity analysis is also recommended that determines the years of known outbreaks from the FIDS record, as well as periods without outbreaks, and then modify the OUTBREAK criteria to improve the detection without causing false positives in other parts of the record.

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