Climatic Drivers of Western Spruce Budworm Outbreaks in the Okanogan Highlands

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CLIMATIC DRIVERS OF WESTERN SPRUCE BUDWORM OUTBREAKS IN THE OKANOGAN HIGHLANDS

By

Todd M. Ellis

Accepted in Partial Completion

of the Requirements for the Degree

Master of Science

Kathleen L. Kitto, Dean of the Graduate School

ADVISORY COMMITTEE

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MASTER'S THESIS

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Todd M. Ellis

June 6, 2016
CLIMATIC DRIVERS OF WESTERN SPRUCE BUDWORM OUTBREAKS IN THE OKANOGAN HIGHLANDS

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Todd M. Ellis
June 2016
ABSTRACT

The western spruce budworm is recognized as the most ecologically- and economically-damaging defoliator in western North America. Like other defoliating insects, the western spruce budworm consumes the needles of host tree species like the Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), causing limb and tree mortality, regeneration delays, and reduction in tree growth rates. Synchronous western spruce budworm outbreaks can occur over much of a host species' range, and we need a better understanding of the mechanisms driving the species’ population dynamics in order to predict climate change effects, mitigate ecological and resource management impacts, and understand ecosystem dynamics. To contribute to our understanding of this species' outbreak dynamics, we used dendrochronological methods to reconstruct multicentury outbreak records for four sites in the Okanogan Highlands of central Washington State. By comparing these reconstructed records to historical and reconstructed regional drought data, we were able to test drought history as a potential driving factor of western spruce budworm population dynamics, as well as see how human impact may be affecting these population dynamics. Outbreak synchrony was found to increase after the late 19th century, possibly due to anthropogenic factors. This change is more readily apparent as the intensity of outbreaks increases. Drought records show that outbreaks tend to occur as the drought severity decreases, and moisture availability increases. As the variability of climate conditions is projected to increase, trending towards warm and dry conditions, the intensity and frequency of high-intensity western spruce budworm outbreaks could likely increase as well.
ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Aquila Flower, for her unending enthusiasm, guidance, and mentorship both in the field and lab. I would also like to thank my committee, Drs. Andy Bunn and Michael Medler for their support and feedback in building this project. Paul Nash and Connie Mehmel of the USFS both contributed essential knowledge of the Okanogan Highlands study area. Dr. Daniel Gavin of the University of Oregon provided important feedback on our methods. Lastly, this project would not have been possible without the field and lab assistance of Marissa Bhatnagar, Branden Rishel, Christopher Zemp, Venice Wong, Ryan Schumacher, Shelby Van Arnam, Demian Estrada, Derek Huling, and Dustin Greaves.
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1. INTRODUCTION

Western spruce budworm (*Choristoneura occidentalis* Freeman) is recognized as the most ecologically- and economically-damaging defoliating insect in western North America (Fellin & Dewey 1986). Regionally synchronous, decade-long outbreaks over large regional areas lead to widespread ecological resource impacts. However, the causal mechanisms driving this species’ outbreak patterns and population dynamics remain under-explored, with results often pointing to contradictory mechanisms. An understanding of the western spruce budworm’s (WSB) population dynamics is necessary in order to understand ecosystem dynamics, predict climate change effects, and mitigate ecological and resource management impacts (Swetnam & Lynch 1993; Swetnam et al. 1995; Ryerson et al. 2003; Campbell et al. 2005; 2006; Maclauchlan et al. 2006; Speer 2010; Alfaro et al. 2014; Flower et al. 2014). Multi-century records are needed to establish accurate outbreak histories and shed light on climatic drivers of WSB’s outbreak dynamics. Observational records of WSB activity are only available back to the mid-20th century, but variations in the width of annual tree rings can serve as a proxy record of WSB defoliation. Dendrochronological records have been used to reconstruct multi-century histories of WSB outbreak dynamics in the American Southwest (Swetnam & Lynch 1989; 1993), central Rocky Mountains (Ryerson et al. 2003), and the Pacific Northwest, including British Columbia (BC) and the states of Montana, Idaho, and Oregon (Swetnam et al. 1995; Flower et al. 2014a; Axelson et al. 2015). A prominent gap in the spatial coverage of these outbreak records exists in northern Washington State. In this paper, we present a dendrochronological reconstruction of
WSB outbreaks in Washington State’s Okanogan Highlands region.

The WSB consumes buds and foliage of host trees, with a preference for current-year spring growth, causing reduction in growth rates, regeneration delays, and limb and tree mortality after several years of repeated defoliation (Alfaro et al. 1982; Van Sickle et al. 1983; Fellin & Dewey 1986). While Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the WSB’s principal host species, WSB can also thrive on the needles of true fir (*Abies*) species, including grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), subalpine fir (*Abies lasiocarpa* Hook.), and corkbark fir (*Abies lasiocarpa var arizonica* (Merriam) Lemm.). Additionally, species such as Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), western larch (*Larix occidentalis* Nutt.), blue spruce (*Picea pungens* Engelm.), and white spruce (*Picea glauca* (Moench) Voss) are occasionally susceptible, with other typically non-host coniferous species only susceptible under extreme circumstances (Furniss & Carolyn 1977; Fellin & Dewey 1986). Repeated outbreaks ultimately modify the composition and structure of forests, redistributing the biomass and resources of susceptible host stands by removing photosynthetic tissue and reducing the local carbohydrate supplies necessary for continued growth (Alfaro et al. 1982; Ferrell & Scharpf 1982; Ryerson et al. 2003; Bulaon & Sturdevant 2006; Campbell et al. 2006).

Defoliation occurs during the species’ second instar stage between May and June (Fellin & Dewey 1986). WSB larvae feed on host trees’ needles, staminate flowers, and developing cones, leading to reduced seed production and regeneration capabilities (Fellin & Dewey 1986). Young stands and seedlings, in particular, suffer increased mortality rates and stem deformities following infestations of at least three years, with the level of damage directly related to larval
density and the infestation duration (Fellin & Dewey 1986; Maclauchlan et al. 2006). Mature host stands are most at-risk for suffering topkill and stem deformities, but may also be impacted by increased mortality rates in severe outbreaks (Fellin & Dewey 1986). All infested host stands suffer a loss of biomass, and may have increased susceptibility to subsequent insect outbreaks and pathogens (Alfaro et al. 1982; Ferrell & Scharpf 1982; Hadley & Veblen 1993; Woods et al. 2010).

WSB outbreaks tend to occur synchronously over much of the primary host species’ range, affecting forest stands from southern BC, Canada, to the southern Rocky Mountains in New Mexico, USA (Fellin & Dewey 1986). Large regions of synchronous or near-synchronous WSB outbreaks are usually attributed to one or more of the following factors: adult moth dispersal, exogenous stochastic factors such as climate, or trophic interactions with similarly-synchronous or mobile populations (Myers 1998; Williams & Liebhold & Kamata 2000; Liebhold et al. 2004; Cooke et al. 2007). Dispersal capabilities strongly influence synchrony of population fluctuations at finer spatial scales (i.e., under 200 km), whereas climatic controls may be more a more important driver of synchrony at coarse spatial scales, though the mechanisms behind observed patterns of synchrony are still not well understood (Peltonen et al. 2002).

Local weather conditions can affect WSB populations, particularly during spring emergence. WSB populations emerge prior to their hosts' annual bud-flushing, and rely on a mixture of the previous years' needles, dispersal to areas with current-year bud-flush, or, preferentially, pollen cones produced mostly by older trees early in the season, that bridge the gap between spring emergence and bud flush (Blais 1952; McGugan 1954; Greenbank 1963; Sanders 1991; Shepherd 1992; Nealis & Lomic 1994; Trier & Mattson 1997; Nealis & Nault
If temperatures are too warm, they may promote an earlier emergence for WSB larvae, which leads to local population reductions when larvae either starve or disperse to find food (Thomson & Moncrieff 1982; Shepherd 1983; Chen et al. 2003; Thomson & Benton 2007). Dispersal of larvae is particularly risky in relatively low density stands, where larvae must traverse greater distances between tree crowns in order to find suitable food (Miller 1958; Nealis & Lomic 1994; Nealis & Régnière 2009). Similarly, temperatures that are too cold can cause high mortality rates by freezing larvae or the foliage they feed on (Fellin & Schmidt 1973; Wulf & Cates 1987).

During outbreak conditions, earlier WSB instar emergence leads to a rapid decrease in pollen cone production (Blais 1952; Nealis et al. 2003; Hughes et al. 2014), which Douglas-fir compensates for by producing more vegetative buds (Shepherd 1992; Nealis & Régnière 2004). Despite this, a higher number of WSB emerging earlier in the season still rapidly reduces needle density (Nealis & Régnière 2009). Late-feeding WSB are thus subject to reduced rates of survival and fecundity, as well as dangerous weather conditions like high winds or storms (Campbell 1993).

In the Pacific Northwest, WSB infestations are frequent in many coniferous stands, with insect populations often continuously present at low endemic levels (Swetnam et al. 1985; Fellin & Dewey 1986; Wickman 1992). Radial growth impacts from WSB outbreak defoliation tend to last, on average, between 11 and 15 years (Lynch 2007). Aerial survey records suggest even shorter intervals of WSB outbreaks, lasting as few as one to two years in some regions (USDA Forest Service 2014). Quiescent period durations also vary across impacted regions, with an average of 32 to 40 years between outbreaks (McCune 1983; Anderson et al. 1987; Swetnam & Lynch 1989; 1993; Swetnam et al. 1995; Weber & Schweingruber 1995; Ryerson et al. 2003;
Campbell et al. 2006; Lynch 2007).

Recent records suggest the Pacific Northwest has been impacted by a widespread outbreak since the 2009 season (Man 2012), though the WSB may be undergoing population crashes in many regions. For 2013, Oregon State reported only 129.5 hectares (ha) of defoliated vegetation, down from 2012’s 32,022.8 ha, and Washington State reported 72,794.9 ha defoliated, down from 206,871.3 ha the previous year, and the lowest recorded since 2003 (Jenkins 2015). Isolated mid-elevation Washington forests like those of the Okanogan Highlands remained heavily infested throughout 2013, and even continued a 3-year increasing trend across Colville National Forest (Jenkins 2015). BC's central and southern interior regions house a similar, connected topography and climate to Washington's mid-elevation forests. Washington's Okanogan Highlands and nearby forested regions such as the Kamloops and Cariboo Forest Regions have experienced similar outbreak histories according to historical records and have sustained heavy outbreak conditions in recent years (Alfaro et al. 2014; Axelson et al. 2015). Like much of the Western US, overall WSB defoliation damage appears to be decreasing in the BC regions. Aerial survey records for 2014 suggest a total of 44,608 ha were defoliated by the WSB with a minor margin for error, the lowest recorded level since 2000's 22,851 ha (Westfall & Ebata 2014).

Over the course of the 20th century, some regions have shown increasing outbreak synchrony, severity, and/or intensity, possibly as a result of human impact (Anderson et al. 1987; Swetnam & Lynch 1989; 1993; Swetnam et al. 1995; Ryerson et al. 2003; Campbell et al. 2006; Flower et al. 2014a; 2014b). These changing outbreak dynamics may be linked to expansion of the extent and predominance of WSB’s host species due to historical human impacts. Selective
harvesting of competing species, fire exclusion, and livestock grazing are thought to have
favored the establishment of WSB’s host species (Anderson et al. 1987; Wickman 1992; Mutch et al. 1993; Hessburg et al. 1994; Keane et al. 2002). Human land-use habits have led to a dense
multilayered canopy structure, promoting the growth of relatively shade-tolerant species like
Douglas-fir. The increased density of sub-canopy trees provides additional habitat for the WSB (Maclauchlan & Brooks 2009)

Historical documents in the Pacific Northwest record WSB outbreaks as early as 1909 in
the Vancouver Forest Region of BC (Harris et al. 1985). For the western United States, annual
Insect and Disease Surveys (IDS) have been provided by the USFS since 1947, though the
accuracy for outbreak records is questionable until to more recent decades (Fellin & Dewey
1986; Williams & Birdsey 2003; Speer 2010; USDA Forest Service 2014). Historical outbreak
records report a widespread, untreated outbreak period from 1942–1948 (Brookes et al. 1987).
Aerial survey records did not start until the IDS was initiated in 1947, and recorded no outbreaks
between the widespread 1940s outbreaks and smaller, site-specific occurrences in the 1970s
(USDA Forest Service 2014). More accurate ground survey records didn’t monitor WSB
outbreaks until 1976–1977, and only monitored the western border of the Okanogan Highlands
region near Mt. Hull (McComb 1979). These outbreak dates were not reflected in aerial survey
records. WSB populations were noted as present throughout the Okanogan National Forest and
neighboring Colville National Forest in 1975 and 1976, but were not closely monitored for
management (USDA Forest Service 1977). McComb’s (1979) data followed widespread DDT
treatment for a severe Douglas-fir tussock moth (Orgyia pseudotsugata McDunnough) outbreak
from 1970 to 1974, notable for being the last official use of DDT on USFS land (Mehmel,
personal communication 2015), as well as treatment with malathion in 1976 and zectran in 1977.

Climatic variables are thought to be a primary driving force of WSB population dynamics (Campbell 1993; Swetnam & Lynch 1993; Swetnam et al. 1995; Murdock et al. 2013; Flower et al. 2014a). Due to this, climate change is expected to affect the range of WSB and associated outbreak characteristics like frequency and intensity (Swetnam & Lynch 1993; Murdock et al. 2013). A warming climate could potentially increase the area susceptible to WSB infestations by moving WSB populations to higher elevations and latitudes as host tree ranges shift upwards and northwards (Logan et al. 2003; Maclauchlan et al. 2006; Woods et al. 2010; Murdock et al. 2013). Fluctuations in moisture availability are seen as the most important variable in effecting changes to WSB population dynamics (Hard et al. 1980; Thomson et al. 1984; Campbell 1993; Swetnam & Lynch 1993; Ryerson et al. 2003; Flower et al. 2014a). WSB response to climate variables is inconsistent across many regions, however. For instance, Swetnam & Lynch (1993) suggested high spring precipitation as an influencing factor in outbreak timing in Colorado, while Flower et al. (2014a) found an increase in moisture stress was necessary in initiating outbreaks in Oregon, Idaho, and Montana. The potential range of the WSB includes a variety of climatic zones over multiple state lines, with controlling climatic variables likely differing based on local- and regional-level climate. Three hypotheses have been proposed to explain the observed relationships between insect populations and moisture availability: The plant stress hypothesis proposed that sustained abiotic factors like drought fuel insect outbreaks by concentrating nutritional quality in foliage (White 1984; Mattson & Haack 1987). The plant vigor hypothesis is a competing hypothesis suggesting high moisture availability can sustain outbreaks by improving both the quality and quantity of foliage (Price 1991). The most recent hypothesis proposes instead that a nonlinear combination of factors, like temporal variability in
moisture stress, would be required to initiate and subsequently sustain insect outbreaks (Huberty & Denno 2004; Mody et al. 2009).

Multi-century outbreak reconstructions of at least three centuries are necessary to better understand the population dynamics of the WSB. The development of additional multi-century reconstructions contributes to the continued development of forest management strategies that can cope with the economic and ecological impacts of defoliating insects (Shepherd 1994). The purpose of this study is to uncover the regional history of WSB outbreaks in the Okanogan Highlands region, connecting an important geographic gap to surrounding reconstructed outbreak records (e.g., Flower et al. 2014a; Axelson et al. 2015). Additionally, we characterize the frequency, periodicity, levels of synchrony, and intensity of the region's outbreak history. Using these data with historical and reconstructed climate records, we enhance our understanding of how climate variables like moisture availability contribute to the WSB's population dynamics, and the importance of understanding how our changing climate will likely lead the changes we are witnessing in WSB outbreak patterns.
2. METHODS

2.1 Study Area

We collected samples at seven sites in the Okanogan Highlands of Okanogan National Forest in August 2014 (Fig. 1). The Okanogan Highlands are characterized by an arid, shrub-steppe environment, with vegetation dominated by Douglas-fir, with lesser amounts of ponderosa pine (*Pinus ponderosa* Douglas ex P. & C. Lawson), western larch, and grand fir (McNab & Avers 1994). Elevations at our sites ranged between 1000 and 1600 m. The geological setting of most study sites was gneiss bedrock, with the easternmost host site identified as basalt (Lasmanis & Cheney 1994). We used ClimateWNA to find instrumental, historical climate conditions associated with each site's coordinates. Using the 30-year climate normals for 1981–2010, the mean center of our sites reports average temperatures between from -6.1°C to 17.1°C in the coldest and warmest months, respectively; annual precipitation was recorded as 433 mm, with 160 mm occurring during summer months (Daly et al. 2002; Wang et al. 2012).

2.2 Sampling Strategy

We collected samples at paired host and non-host sites. Samples collected at non-host sites were used to create a control chronology to compare host chronologies against. This approach allowed us to isolate the defoliation signal contained in host tree-ring chronologies. We chose Douglas-fir as a host species due to its wide range in the Okanogan Highlands and its susceptibility to WSB outbreaks (Little 1971; Mason et al. 1997). We chose ponderosa pine as our non-host species. Douglas-fir and ponderosa pine have overlapping geographic ranges and similar responses to climate, but ponderosa pine is rarely defoliated by the WSB (Critchfield &
Little 1966; Fritts 1974; Swetnam et al. 1985; Swetnam 1987; Watson & Luckman 2002; Littell & Tjoelker 2008; Chen et al. 2010; Griesbauer & Green 2010).

We selected potential study areas with a history of frequent WSB outbreaks based on annual USFS Insect and Disease Survey data (USDA Forest Service 2014, Williams and Birdsey 2003). Within those potential study areas, we selected specific study sites using satellite imagery and *in-situ* evidence. We selectively targeted sites for their distance from active forest service roads and from one another, with significant topographic features such as mountains or valleys ideally separating sites. We targeted stands with multi-century records, with the oldest trees ideally dating to at least 300 years (Table 1). We avoided host and non-host stands with extensive recent disturbances such as logging or fire damage.

We extracted two increment cores per tree. We avoided reaction-wood by coring parallel to the slope contour at 1.3 meters above ground, except where impossible due to difficult topography (Speer 2010). We sampled between fifteen and twenty trees from each of our four host stands in order to adequately cover the regional history (Table 1). Within sites, we selectively-sampled based on visual assessment, using criteria that included old-age cues such as flattened tops, spiral-grained bark, large lower limbs, and the diameter at breast height (DBH) being at least 40 cm. We avoided samples that included any indication of significant damage (e.g., fire scars) that could potentially distort the growth patterns.

For non-host stands, we sampled between six and seventeen trees from three sites to maximize the visible impacts of defoliation. To produce the longest possible record, we collected non-host samples with the intention of creating a single regional chronology for use with each host site. Monospecific non-host stands were preferentially targeted in order to avoid any growth release from species affected by defoliation or competition (Swetnam et al. 1995). Old-growth
 ponderosa pine stands are, however, aggressively-maintained by the USFS, which made locating suitable non-host stands difficult (Nash, personal correspondence 2014). Because of this, the age of non-host stands superseded the importance of monospecificity and we include six trees from our Turner Lake site despite the presence of Douglas-fir.

2.3 Sample preparation & laboratory analysis

We prepared our samples using standard dendrochronological techniques (Stokes & Smiley 1968; Fritts 1976; Speer 2010). We dried and glued core samples to wooden core mounts before surfacing with 120-, 220-, 320-, 400-, and 600-grit sandpaper. With polished samples, we first visually crossdated each sample from the bark inwards using a microscope. We then scanned and measured to the nearest 0.001 mm using Cybis' CooRecorder and CDendro software (Larsson & Larsson 2014). We used CDendro to visually identify known outbreak periods (Swetnam et al. 1985; 1995), and create master chronologies for each host and non-host site. CDendro allowed for the creation of a master chronology to be used with any sample measurements, minimizing the errors caused by our visual interpretation (Larsson & Larsson 2014).

The R package dplR contained functions to generate skeleton plots and cross-correlate our time series with a master chronology, which were necessary in locating errors with our measurements and missing rings prior to detrending (Bunn 2008; Bunn et al. 2012; R Core Team 2013; Bunn et al. 2015). We used an additional ponderosa pine chronology from the International Tree-Ring Data Bank (ITRDb) archives during non-host crossdating for years prior to 1976 (Brubaker 1976). This archived chronology was not used in our final analyses because
we needed chronologies that would cover late 20th century outbreak periods.

We used the dplR package to detrend raw measurements for host and non-host sites using a 100-year cubic smoothing spline (Cook 1985; Bunn 2008; Bunn et al. 2012). This method of standardization ensures decadal impacts like WSB outbreaks will be maintained, while correcting for year-to-year age-related growth trends (Fritts 1976; Cook 1985; Cook & Holmes 1986; Swetnam & Lynch 1993). A few samples with abnormal growth trends, including overly-complacent or parasitized specimens, were removed from the study prior to detrending. Resultant ring-width indices were averaged together by tree, and used to create mean site chronologies for host and non-host sites. A principal components analysis was run on the standard and residual non-host chronologies to extract the common, presumably climatic, signal shared by the non-host trees. We chose the first principal component of our three standard non-host master chronologies for our outbreak reconstructions, because it explained the highest variance (81%) and correlated most strongly with our host chronologies.

For climate records, we used both instrumental, historical climate division data for periods after 1895 (Wang et al. 2012), and reconstructed Palmer Drought Severity Index (PDSI; Palmer 1965) records for complete multicentury series through 2003 (Cook et al. 1999; 2004). We conducted a Pearson’s cross-correlation analysis on the host and non-host chronologies against regional instrumental and reconstructed records to determine whether the chronologies expressed the similar climate responses necessary for outbreak reconstructions (Fritts 1974; Cook 1999; Cook et al. 2004; Wang et al. 2012).

2.4 Outbreak Reconstructions

We visually compared ring-width measurements with historical records of known outbreak periods within the Okanogan Highlands and nearby dendrochronological reconstructed...
outbreak dates (e.g., Campbell et al. 2006; Flower et al. 2014a; Axelson et al. 2015). Like crossdating, this visual comparison provided us with a first step to identifying periods of growth suppression at tree-level. Outbreaks are often visible as long-term growth suppression periods in the host tree chronologies that are not apparent in the regional non-host chronology. To statistically-reconstruct outbreak records, we first subtracted climatic noise from each host tree using the equation:

$$Corrected\ Index = I_{ht} - \frac{\sigma_h}{\sigma_n} (I_{nt} - \bar{I}_n)$$

where $I_h$ is the host trees' ring-width index for each individual year ($t$), $\sigma_h$ and $\sigma_n$ are the standard deviations of the individual host tree series and the regional non-host series' common period, $I_n$ is the non-host control index for each year ($t$), and $\bar{I}_n$ is the mean for the non-host index for the common period. The output of this equation created a new value for each year of growth across host trees, where positive or negative values represent growth above or below the expected growth from climatic factors alone (Nash et al. 1975; Swetnam et al. 1985; Campbell et al. 2006). Similarities between the corrected site indices during their shared common periods (1719–2014 for three sites, 1796-2014 for all four) were checked using Pearson's correlation coefficients.

To develop a regionally appropriate set of criteria for identifying WSB outbreaks, we normalized the corrected tree series and identified outbreak-length periods of low growth. We did not record non-consecutive years of positive growth as outbreak interruptions, as non-consecutive positive growth years are common within outbreak periods (Swetnam et al. 1995; Campbell et al. 2006). Minimum thresholds for WSB outbreak length vary by region, typically ranging between four to eight years of sustained below-average growth, with at least one year of growth at least 1.28 standard deviations below the long-term mean ring width (Swetnam et al. 1995; Campbell et al. 2006).
Another defoliating insect, the Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough), can create similar outbreak patterns in Douglas-fir ring width records, but their outbreaks last only three years, which makes four-year outbreak durations the shortest desirable outbreak length for separating the WSB signal from similar defoliating insects (Brubaker 1978; Brubaker & Greene 1979; Wickman et al. 1980; Wickman 1986; 1992; Swetnam et al. 1995; Mason et al. 1997). We tested a minimum outbreak duration criterion of between four and eight years to resolve which most accurately covered historical outbreak records, with four years being deemed the most reflective of historical outbreaks. A minimum growth reduction severity criterion of 1.28 standard deviations below the long-term mean was used for all reconstructions. Outbreak periods were identified based on these criteria for each individual tree, resulting in an annually resolved binary record of outbreak / non-outbreak conditions.

We standardized the binary, tree-level outbreak data into the percentage of a site's sample population reporting infestation year-to-year (e.g., Campbell et al. 2006). Since outbreak reconstructions tend to regularly report some level of tree infestation reflecting endemic WSB populations, small-scale population changes, or background noise, we explored multiple outbreak intensity thresholds between 30-80%. We compared the resultant outbreak time series with historical air and ground survey records, with which a 40% threshold best identified the start of moderate outbreak conditions (McCune 1979; Westfall & Ebata 2014; Axelson et al. 2015; Jenkins 2015; Mehmel, personal correspondence 2015). Additionally, we used thresholds of 60% and 80% to identify high and very high outbreak intensities, respectively, which could gauge how intensity patterns have changed over the entire time series. The resultant corrected chronology provides measures of synchrony (the amount of trees per site that show an ongoing
infestation), duration (the length of time when growth was below the corrected indices' potential growth), and intensity (the maximum growth reduction in an outbreak) of outbreak disturbances within and between stands (Swetnam & Lynch 1993). We defined a chronology for regional outbreaks by periods in which at least two of our four sites recorded coincident outbreaks for a minimum of two back-to-back years.

2.5 Statistical Analysis

2.5.1 Outbreak Characteristics

We averaged outbreak duration and intensity for site and regional outbreak records, and checked for temporal changes by separating both duration and intensity data by century. Since the use of centuries as a break-point feels arbitrary, we also divided the data into two similar-sized groups: Before 1870 and after 1869. This separation would also roughly coincide with western expansion and the introduction of controlled forestry practices. As historical records prior to 1970 either aren't reliable or don't exist for our study area, this breakpoint provides a loose representation for when Euro-American settlers’ influences may have begun most affecting regional outbreak patterns (Johnson & Ross 2008). Kruskal-Wallis nonparametric ANOVA was performed on the normalized corrected indices to test for differences between Douglas-fir’s growth response during and outside of outbreak conditions (Burt et al. 2009).

2.5.2 Outbreak Synchrony Among Sites

We assessed the level of synchrony between site events using Pearson's correlation coefficient. Despite the high autocorrelation inherent in synchrony records, which makes estimation of statistical significance unreliable, the correlation coefficients can be used as an approximate index of sites' outbreak synchrony over time (Buonaccorsi et al. 2001). This simple analysis was conducted on the percent of each site recording outbreaks across our four sites'
common period (1796–2014). We also separated the common period around the 1870 breakpoint to get a rough estimation of how site interactions may have changed before and after major human impacts began affecting the region. We used a modified one-dimensional Ripley's K-function (Ripley 1976; Gavin et al. 2006) to test whether discrete outbreak events were independent of one another over increasing bidirectional temporal lags. Years of outbreak occurrences, initiations, and cessations for our three oldest sites' common period were input into K1D v1.2 software (Gavin 2010). The youngest site, SMD, was removed from this method in order to retain as much of our regional record as possible without sacrificing too much of our sample size. This method uses designated temporal step size—e.g., 1 year—to check for co-occurrence of outbreaks between any of the sites over increasingly long temporal windows until the bidirectional window is half the length of the total record length, with the resultant K and L functions providing a measure of outbreak synchrony or asynchrony over increasing temporal scales. To test for statistical significance, we ran 1000 simulations with a .95 confidence envelope using a circular randomization, with random year data added to all site records. We also ran this to test for differences between our early and latter periods for all three of our intensity thresholds -- i.e., moderate (40%), high (60%), and very high (80%).

2.5.3 Climate-Outbreak Associations

To identify climatic conditions associated with WSB outbreak initiations and cessations, we used superposed epoch analysis and t-tests at both stand- and region-levels (Lough & Fritts 1987; Grissino-Mayer 2001). PDSI records were used as a measure of summer (i.e., between June and August) moisture stress using soil type, precipitation, and temperature (Palmer 1965). We tested both historical (1895–2014) and reconstructed (1685–2003) PDSI (Cook et al. 2004) records, as well as historical precipitation data for water-years (i.e., previous October to current
September) and growing years (April to September of the current year). Instrumental records for the Okanogan Big Bend (Climate Division 7) area were provided by the National Oceanic and Atmospheric Administration's (NOAA) National Centers for Environmental Information (NOAA 2015). Cook et al.’s (1999; 2004) multi-century, gridded PDSI reconstruction data was built from tree-ring chronologies provided by the ITRDb. The North American reconstruction network is available for 2.5° by 2.5° gridcells, with our regional data drawn from grid 43 (Cook et al. 1999; 2004).

We conducted paired, two-sample t-tests to test for differences between PDSI data associated with outbreak conditions against non-outbreak conditions; PDSI data two years before outbreaks against both PDSI during outbreak and non-outbreak conditions; and PDSI data two years before outbreaks and during outbreaks against PDSI during non-outbreak conditions. We used superposed epoch analysis to identify patterns of climatic conditions associated with outbreak initiation and cessation dates. Superposed epoch analysis uses event years with time series data and designated temporal lags to test for significant departures from the mean (Grissino-Mayer 2001). Event years for our study were designated as either outbreak initiation or cessation dates. We defined initiation dates as the first of two or more consecutive years recording an outbreak following a gap of at least two years without recorded outbreaks, and cessation dates as the first of at least three years of non-outbreak conditions following an outbreak (Flower et al. 2014a). A window of five years before and after host site's event years was used in conjunction with both historical and reconstructed climatic data to check for potential outbreak associations. Statistical significance was assessed by performing 1000 Monte Carlo simulations using dplR (Bunn 2008; Bunn et al. 2012).
3 RESULTS

3.1 Dendrochronological characteristics and Outbreak histories

A total of 69 host trees and 32 non-host trees were sampled over our six sites. Our regional non-host chronology dated to 1685. Host sites had records from at least two trees starting between 1685 and 1796 (Table 1). Interseries correlation (Pearson's $r$; $p < 0.01$) for our host sites ranged between 0.650 and 0.780, while non-host sites ranged between 0.627 and 0.760. Correlation coefficients (Pearson’s $r$) between our chronologies (both standard host site and regional non-host) and climate data supported the use of our sites for outbreak reconstructions (Table 2). All of our host site chronologies, as well as our regional non-host chronology, reported significant ($p < 0.05$), positive relationships with reconstructed and historical PDSI, as well as water-year precipitation for the current and preceding year. The relationship with temperature returned less significance, although the current growing-year’s temperature had a significant, negative relationship with all but one of our host sites (Table 2).

Outbreak durations ranged from two to 19 years across sites, with site mean outbreak durations ranging between 8.6 and 10.7 years by site (Table 3). Quiescent periods lasted between four and 52 years, with site means ranging between 11.4 and 20.0 years. The average for the regional outbreak duration and quiescent period length was 9.2 and 14.6 years, respectively. During the 330-years covered by our regional reconstruction (1685–2014), all reporting sites experienced identical outbreak conditions (either outbreak or non-outbreak) during 184 years (55.8%). There were a total of 16 regional outbreaks (i.e., periods in which at least two sites share concurrent outbreak conditions) covering 130 years (39.4%) of the total 330 years. All four of our sites showed changes between the early (1685–1869) and modern (1870–2014) periods,
with an increased number of years reporting outbreaks in the modern period.

### 3.2 Inter-site outbreak synchrony

Outbreak and non-outbreak conditions tended to occur synchronously or near-synchronously (Fig. 2). Our regional outbreak record (i.e., two or more concurrent site outbreaks) showed the strongest shift to higher synchrony and intensity in the modern period (Table 4). With our moderate intensity threshold, the early period included 43.8% of regional outbreaks, and the modern period 56.2%. Our very high intensity threshold contained all of its regional outbreaks in the modern period, with only three recorded outbreaks initiating in 1938, 1992, and 2010. Based on the moderate outbreak threshold, there has been little to no change in outbreak synchrony since the start of the reconstruction. However, analysis using higher intensity thresholds, revealed an increase in high-intensity, synchronous outbreaks in the modern period (Table 4). Very high outbreak intensities for our three oldest sites showed between 0.0% and 5.9% of the early period records returning outbreaks, and between 6.9% and 14.5% of the modern period represented by outbreaks.

Pearson's correlation of outbreak histories also revealed a pattern of synchrony. The average inter-site correlation for the three oldest sites' outbreak histories (i.e., MPD, TMD and VLD) was 0.60, while all four sites yielded a correlation of 0.71. The Tunk Mountain Douglas-fir (TMD) reduces both periods' correlations likely due to a unique period of asynchronous, stand-specific outbreaks during the mid-19th century also recorded in nearby outbreak reconstructions (Fig. 2; Harris et al. 1985; Campbell et al. 2006; Axelson et al. 2015).

The modified one-dimensional K-statistic for all outbreak years of both common periods showed a high statistical significance (at the 0.05 confidence level) for levels of bidirectional temporal synchrony for up to seven years for our two oldest sites, 11 years for our three sites.
dating to 1719, and 22 years when analyzing records across all four sites (Fig. 4). Initiation and
cessation dates for the 1719 common period showed significant temporal synchrony up to six
and nine years, respectively, with a higher degree of synchrony for initiation events than
cessation dates or all outbreak years (Fig. 3). With increasing outbreak intensity, synchrony was
highly-concentrated in the late period (1870-2014). In the early period (1719-1869), no
significant synchrony was found for outbreaks using our high and very high outbreak intensities
(Figs. 5 & 6). All outbreak intensities reported between up to 9 to 24 years of synchrony for the
late period records.

3.3 Climatic influences on outbreaks

Outbreak initiation dates were preceded by between two and five warm-dry years
at all sites, with initiation dates tending to occur in cooler, wetter years (Fig. 7). While no site
reported statistically-significant cool-wet years in the five years following an initiation event, all
sites still showed a shift towards cool-wet conditions. Our regional outbreak record (1685–2014)
shows a statistically-significant warm-dry anomaly in the second year preceding initiation events
(Fig. 8). Paired, two-sample t-tests revealed significant ($p = 0.01$) differences between PDSI
values occurring during outbreak years and PDSI values occurring during non-outbreak years
(Table 5). The PDSI values that occurred in the two years preceding outbreak years had more
similarities with PDSI values occurring during non-outbreak years ($p = 0.33$) than those
occurring during outbreak years ($p = 0.06$). Including the PDSI values from the two years
preceding outbreak events with those occurring during outbreak conditions retained significant
($p = 0.02$) differences from PDSI during non-outbreak conditions.

We identified a tendency for shifts from cool-wet to warm-dry conditions during
outbreak cessation years (Fig. 7). Between three and four sites reported cool-wet conditions in
each of the five years preceding outbreak cessation dates, with two of our sites reporting at least one significant year of cool-wet conditions. Two of our four sites reported statistically-significant cool-wet years preceding a cessation date. Our analysis of regional outbreaks shows the same pattern, with cool-wet conditions shifting to warm-dry conditions one year prior to the cessation date.

We saw the same pattern for historical PDSI data (1895–2014) from climate station records, which show a transition of dry-warm conditions to cool-wet conditions (Fig. 9). All sites reported warm-dry conditions for at least three years in a five-year window preceding outbreak initiations, with one site reporting significance for three years. Following outbreak initiations, all sites reported cool-wet periods for at least two years in the five-year window, with three sites reporting significant cool-wet conditions. Three out of four sites reported warm-dry conditions during outbreak initiation events. All sites reported warm-dry conditions at least once in the two years following outbreak initiations, with one instance of significance. The regional outbreak record exhibits a statistically significant pattern of warm-dry conditions two years prior to initiation events, with significant cool-wet periods between three and five years after initiation dates (Fig. 10). All four of our sites and the regional outbreak record showed between one and four significant years of cool-wet conditions prior to cessation dates using the historical PDSI data, with no sites returning significant conditions following cessation dates (Figs. 9 & 10).
4 Discussion

4.1 Outbreak histories

We were able to successfully reconstruct 330 years of WSB outbreak history for the Okanogan Highlands. Our reconstructed outbreak dates closely match those recorded in historical documents and aerial survey reports. Since regional historical records are only available after the 1970s, nearby historical records for southern BC were used alongside regional records to check against our outbreak reconstructions. Harris et al. (1985) records WSB outbreaks in the Cascade Range for the 1923–1930, 1943–1958, and 1977–1983 periods, with only the earliest outbreak period not reflected in our data. Data were not recorded for the region between 1931 and 1942, possibly explaining the discrepancy between our reconstructions and historical records. The three most recent outbreaks (1975–1983, 1990–2001, 2009–present) concur with the regional insect survey data and other WSB outbreak studies from the Pacific Northwest. USFS reports in the late 1970s indicate initiating outbreaks starting between 1974 and 1976 in and west of the Mt. Hull area of the Okanogan Highlands, which matches our initiation year for the 1975–1983 outbreak (USDA Forest Service 1977; McComb 1979). This outbreak period was not reflected in the aerial survey data (USDA Forest Service 2014). Aerial survey data reported a subsequent outbreak between 1986–1993, while our regional reconstruction reported an outbreak between 1990–2001, which is concurrent with nearby BC records reporting outbreaks throughout the 1990s (Alfaro et al. 2014; Axelson et al. 2015).

Our ongoing regional outbreak reported an initiation date of 2009, while aerial survey data report outbreaks starting in 2008 (USDA Forest Service 2014). Westfall & Ebata (2014) has provided annual coverage of severe WSB outbreaks in nearby Okanagan and Merritt Timber
Supply Areas from 2006–2014, while Jenkins (2015) reports a stark increase in defoliated acreage across Washington State starting in 2005–2006. Both reports show significant declines in WSB populations starting in 2013, although Jenkins (2015) suggests a strong population was maintained in the Okanogan Highlands region. This matches our data, as all trees sampled across our sites in 2014 still held active WSB populations. The variable lags or missing data from the aerial survey records in relation to our regional outbreak data and nearby sites’ historical and reconstructed outbreak data may be in part to inconsistent quality control and accuracy in identifying insect outbreaks via aerial survey (Johnson & Ross 2008). Our outbreak reconstructions resulted in outbreak patterns similar to those seen in nearby regions. The regional record’s average outbreak duration of 8.3 years closely matches nearby studies in the Pacific Northwest (Campbell et al. 2006: 12 years; Flower et al. 2014a: 12 years; Alfaro et al. 2014: 7 years; Axelson et al. 2015: 11.2 years), while the regional quiescent period of 13.3 years was the lowest among nearby studies, which ranged between 15 to 64.2 years.

It’s possible our chosen sites are not completely representative of the area, as some limitations are inherent in any dendroentomological study. Swetnam & Lynch (1993) reported five shortcomings of WSB studies: Only surviving trees can be sampled, making it impossible to include mortality in our study; site sample sizes decreased as time increased, negatively impacting the accuracy of our oldest reconstructions; corrected indices must contain some degree of influence from other biological factors and climate, as the nonhost chronology cannot be a perfect control for climate (e.g., Axelson et al. 2015); minor infestations may be lost within the corrected indices, leading us to record outbreaks of moderate to very high intensities; and temporal lags (of one to three years) between the tree’s growth response and either outbreak initiation or cessation dates can be expected. During most years of an outbreak, a progression of
reduced radial growth occurs, often identified in historical records with a lag of one to three years between the initial known infestation and visible annual ring growth suppression (Alfaro et al. 1982; Swetnam & Lynch 1989; Swetnam & Lynch 1993; Mason et al. 1997; Speer 2010; Flower et al. 2014a). This lag is likely a product of the host trees’ abilities to store food reserves in previous years’ xylem and phloem tissue growth (Fritts 1976). Similarly, normal radial growth rates may not return for one or more years following a population crash, ending the outbreak. Visible lags between the observed outbreak cessations and the trees’ recovery are due to the time required for replacing lost foliage (Alfaro & Maclauchlan 1992).

Additionally, our four host sites may not cover enough of the region to represent regional variability for the entire Okanogan Highlands (e.g., Alfaro et al. 2014). Douglas-fir dwarf mistletoe was prevalent in 11 of our sampled trees from MPD and VLD, but no associated growth anomaly could be separated from WSB-caused growth impacts, and external signs of severe Douglas-fir dwarf mistletoe infection also overlap with signs of long-term WSB infestation (Hadfield et al. 2000). Filip et al. (1993) found no significant interaction or effect on mortality when both WSB and Douglas-fir dwarf mistletoe infestations were found, although stands with severe histories of both infestations had the most visible tree mortality. Sala et al. (2010) determined that Douglas-fir dwarf mistletoe did not act as a significant resource sink. The 1975–1983 regional outbreak shows no lag between our reconstruction and historical records for the initiation year, which may be the result of signal contamination by Douglas-fir tussock moth’s regional 1970–1974 outbreak (Mehmel, personal communication 2014). The Douglas-fir tussock moth impacts trees’ growth response similarly to the WSB, which could replace the lag between outbreak initiation and trees’ growth response we expect to see with WSB outbreaks.
(Brubaker 1978).

4.2 Inter-site outbreak synchrony and driving factors

Our reconstructions show that WSB outbreaks have been occurring synchronously in the region back to at least 1685. The regional outbreak records showed 16 instances of synchronous outbreaks occurring between 1685 and 2014. Similar to other studies, our region has seen an increase in outbreak synchrony, likely as an effect of anthropogenic climate change and changing land-use regimes (Swetnam & Lynch 1989; 1993; Swetnam et al. 1995), but not duration or frequency after the 19th century (e.g., Ryerson et al. 2003; Alfaro et al. 2014). The drivers for the high degree of synchrony throughout our outbreak records are not fully understood, but support the influence of fine-scale (i.e., up to 200 km, but strongest up to 100 km) dispersal abilities and exogenous, abiotic stochastic factors on driving WSB and similar insect outbreak synchrony (Williams & Liebhold 2000; Peltonen et al. 2002; Jardon et al. 2003; Liebhold et al. 2004). The latter effect, known as the Moran effect, proposes that the spatial and temporal autocorrelation of abiotic, exogenous factors like PDSI help to synchronize biotic populations over a landscape (Moran 1953).

WSB and similar moths have been found capable of flying hundreds of km in above-canopy winds (Greenbank et al. 1980; Dobesburger et al. 1983; Campbell 1993; Baltensweiler & Rubli 1999), suggesting a moderate dispersal ability limited by geography such as mountainous terrain. Over long distances, dispersal's impact on WSB outbreak synchrony was found to decrease, with Peltonen et al. (2002) finding WSB outbreak synchrony to significantly decrease over distances of 100–200 km. They found that the synchrony of outbreak records decreased at a significantly faster rate than associated weather data, breaking with the assumptions of the Moran effect (i.e., that the degradation of outbreak synchrony and climatic correlations over
distance would follow an identical pattern). Since our sites were all within 50 km of one another, it could be assumed that dispersal plays a role in our outbreak synchrony.

Dispersal abilities are likely influenced by local land-use histories, as well, which have promoted the expansion and growth of Douglas-fir over non-host species like ponderosa pine since the late 19th century. Coupled with fire-suppression, this has led to an increase in host range and canopy density (Anderson et al. 1987; Swetnam & Lynch 1989; 1993; Hessburg et al. 1994; Swetnam et al. 1995; Keane et al. 2002; Maclauchlan & Brooks 2009). This homogenization of host forests could also increase dispersal abilities over smaller areas with limited topographic barriers like the Okanogan Highlands, potentially leading to higher population densities during outbreak conditions (Wilhite & Stock 1983).

Regional climatic stochasticity has still been found to be the dominating influence on insect population dynamics, particularly over larger spatial scales (Williams & Liebhold 1995; Myers 1998; Williams & Liebhold 2000; Peltonen et al. 2002). The loss in dispersal’s influence on population synchrony over distances of 100–200 km is also seen in similar species, and may be more influenced by cyclicity rather than the species’ physiological dispersal capabilities (Sutcliffe et al. 1996; Ranta et al. 1998; Bjørnstad 2000; Williams & Liebhold 2000; Peltonen et al. 2002). Ranta et al. (1999) argued that the classical Moran effect was too log-linear in its explanation, and population synchrony of insects was influenced by nonlinear factors, like a mix of dispersal ability seen in a spatially homogenized landscape, and spatially-autocorrelated climatic patterns. Similarly, some studies have found a spatially heterogeneous landscape leads to reductions in population synchrony (Engen & Sæther 2005). Another potential factor, the influence of trophic interactions on WSB populations, has been underexplored in research, but is assumed as similarly limited to local area due to the mobility of insectivores nearly mirroring
prey dispersal abilities (Peltonen et al. 2002; Jardon et al. 2003). One study of greater Lepidoptera species found increased spatial synchrony among Lepidoptera populations in response to generalist predators (e.g., Campbell et al. 1984), but only with pairs of similar Lepidoptera species sharing a habitat (Raimondo et al. 2005). Studies of parasitoid and pathogen impacts on WSB population dynamics found an increasing chance of mortality as outbreaks move higher in elevation (over 1,000 m) than is historically expected, and increasing landscape homogeneity and biomass allows for denser outbreak populations, which, in turn, promotes the spread of parasitoids and pathogens (Nealis et al. 2009; Nealis et al. 2015). In both studies, parasitoids and pathogens were found as dominating generational mortality factors, causing roughly 33% and 20% mortality in studied populations, respectively, but their impacts during a collapsing outbreak have not been studied.

At our sites, a highly asynchronous period of site-specific outbreaks occurred between 1820–1870, during which only one site (TMD) was impacted by outbreaks. This extended period of asynchrony in the 19th century negatively impacted our Pearson’s correlation values of outbreak histories, particularly evident in the differences between the early and late halves of our outbreak records, where average inter-site correlation for the three oldest sites prior to 1870 was 0.33, but increased to 0.77 after 1869. Without further research, however, it’s unclear how much these correlation values may be impacted by other variables, like changing land-use regimes and dispersal rates. This asynchronous period is also reported by nearby records (Harris et al. 1985; Campbell et al. 2006; Flower et al. 2014a; Axelson et al. 2015), and may be at least partially attributable to alternating regimes of mild warm and cool sea surface temperatures driven by the Pacific Decadal Oscillation between 1840–1923 affecting local teleconnections like PDSI
(Gedalof & Smith 2001).

More significantly, higher-intensity outbreaks at both site- and region-levels reported much higher outbreak frequencies in the last century than in previous centuries. Similarly, the degree of synchrony tended to increase with the intensity threshold used. Our moderate outbreak threshold returned a minor increase of up to three years of significant synchrony in the early period (1719-1869) to up to nine years in the late period (1870-2014). High and very high intensity thresholds returned either no significant synchrony or no synchrony in the early period. All three intensities we investigated shared high levels of synchrony (between 9 and 26 years) in the late period alone. This clustering of synchronous events towards the 20th century suggests the patterns of synchrony we see in the full records (i.e., 1719–2014) for high and very high intensities may not accurately reflect the clustered pattern, due to the method of randomization built into the K1D software (i.e., Bigler et al.'s (2007) Poisson regression intensity weights) being less effective at finding patterns with increasingly-clustered temporal events (Gavin, personal communication 2016). The highest-tested intensity threshold had no regional outbreak events prior to the 20th century, making the degree of frequency and synchrony in the late period unprecedented. Three regional outbreaks of very high intensity occurred among our sites, and all of them in the last century (during the 1940s, 1990s, and 2010s), strongly suggesting anthropogenic impacts such as climate change or land-use practices play a primary role (Swetnam & Lynch 1989; 1993; Swetnam et al. 1995). High intensity-outbreaks have been found to lead to greater levels of dispersal, and consequently higher dispersal losses, after years of particularly severe defoliation (Nealis & Régnière 2009).

4.3 Outbreaks and climatic variability

Climate-growth analysis showed that the annual radial growth rates of both host and non-
host trees were significantly limited by moisture stress (Table 2). Both our host and non-host sites shared similar responses to climatic variables. Similar to Chen et al. (2010), we found positive correlation between our trees’ radial growth and precipitation values, as well as negative correlation with temperature values, which suggests warm, dry conditions inhibit radial growth rates similarly in both ponderosa pine and Douglas-fir, while cool, wet conditions promote radial growth rates.

Initiation dates show a distinct trend of transitioning climate from warm-dry conditions to cool-wet conditions: All four of our sites showed strong warm-dry conditions in the two years immediately prior to initiation events, and three of our four sites held these conditions back to the third year before outbreak initiation events, including one site reporting significantly warm-dry conditions (Fig. 7). During and after initiation dates, climate tended towards cool-wet conditions, which diminished in the second year after the initiation date before returning to synchronous cool-wet conditions among three to four of our sites. This pattern of cool-wet climate conditions during outbreak conditions has been identified by other dendrochronological studies (Swetnam & Lynch 1993; Swetnam et al. 1995; Ryerson et al. 2003; Flower et al. 2014a). Since a lag of one to three years for both initiation and cessation dates usually exists between a tree's radial growth impacts and the actual time of an infestation's initiation or cessation (Alfaro & Machlauchlan 1992; Swetnam et al. 1995; Mason et al. 1997), this suggests that the repeating warm-dry years prior to an outbreak initiation represent the climatic conditions driving WSB outbreak initiations, and the subsequent transition to repeating cool-wet years are necessary to sustain outbreak-level populations. This is consistent with previous studies that found warm-dry conditions as necessary for preceding modern outbreak initiations (Hard et al. 1980; Thomson et
The transitioning climate having a key role in outbreak dynamics supports the nonlinear pulsed plant stress hypothesis (Huberty & Denno 2004; Mody et al. 2009), in which temporal variability in moisture stress was crucial in initiating and subsequently sustaining outbreaks. The competing plant stress and plant vigor hypotheses propose linear factors like sustained drought conditions (White 1984; Mattson & Haack 1987) or excess moisture promoting foliage growth (Price 1991) as being the primary driver for herbivorous insect outbreaks. Moderate drought stress has been found to favor WSB and similar herbivorous insects' growth and reproductive rates, as well as larval survivability, by increasing foliar concentrations of nitrogenous compounds, sugars, and other favorable compounds, particularly in younger trees (Cates et al. 1983; Kramer 1983; Mattson & Haack 1987; Campbell 1993; Parks 1993). This relationship can, however, reverse with prolonged outbreak conditions or increasing outbreak severity (Mattson & Haack 1987; Campbell 1993; Hubert & Denno 2004). These changes to foliage composition over transitioning climate conditions would benefit the growth and survival of WSB during larval stages by favoring the species' diet during moderate drought stress, and subsequently allowing for increased food production (with decreased toughness) during sustained cool-wet conditions (Gower et al. 1992; Krause et al. 1993). Our study follows Flower et al. (2014a) in finding the non-linear relationships of the pulsed plant hypothesis as the strongest explanation for WSB outbreak dynamics over multicentury records, with moisture availability as the primary driving mechanism.

Cessation dates should, like initiation dates, show a one- to three-year lag between years of outbreak conditions and a tree's return to normal growth conditions during the recorded cessation date (Alfaro & Maclauchlan 1992; Swetnam et al. 1995; Mason et al. 1997), which
suggests the five years of sustained cool-wet conditions recorded at three to four of our sites (including two instances of significance) should represent the conditions in which outbreaking WSB populations crashed (Fig. 7). Cessation dates with defoliating species like WSB are typically attributed to a loss of food from sustained overpopulation, and trophic interactions with natural predators, parasites, or pathogens being favored by environmental conditions enough to outperform defoliating insect populations (Cooke et al. 2007; Nealis 2015). As available needles become sparser or difficult to mine, the WSB population density inevitably dips, while predators, parasitoids, and pathogens that prey on WSB are able to maintain population densities and increasingly contribute to WSB population losses (Nealis 2015). Despite also showing a transitioning climate around cessation dates, the transition to warm-dry conditions would not have a causal relationship with the WSB's population crashes. However, since our superposed epoch analysis consistently reported cool-wet conditions at three to four of our sites over five years prior to cessation dates, it’s likely that long-term maintenance of cool-wet conditions plays a causal role in WSB population crashes by feeding significant trophic interactions, food loss, emergence- and budburst-timing, and damaging local weather conditions.
5. CONCLUSION

Western spruce budworm outbreaks have been occurring synchronously in the Okanogan Highlands since at least 1685. Outbreak synchrony across the region has increased in the late period, with synchrony of higher-intensity outbreaks showing the biggest increase in synchrony. Frequency of outbreaks has not changed significantly over the last three centuries, except with high- and very high-intensity outbreaks. Although moderate-intensity outbreaks increased only increased in synchrony, high- and very high-intensity outbreaks saw drastic increases in both frequency and synchrony between the early and late periods, strongly affecting our record of inter-site synchrony and defining the majority of recorded outbreaks over the last century. It’s probable these changes were influenced by changing land-use regimes initiated by western expansion in the 19th century, with impacts like forest homogenization and fire suppression improving the WSB’s dispersal abilities over the spatial scale of our study area.

Our superposed epoch analyses found strong relationships between region- and site-level outbreak histories and moisture availability. Outbreak initiation dates showed a relationship with multiple, consecutive years of low moisture availability in the years preceding initiation events, and consecutive years of high moisture availability during and after initiation years. Cessation dates, on the other hand, showed a strong relationship with high moisture availability during the five years preceding recorded cessation dates. Reconstructed moisture availability data showed a few instances of significant departures of moisture availability preceding either initiation or cessation events, with historical moisture availability records indicating more instances of significant departures preceding and following event years. The temporal variability in moisture
availability occurring during and around outbreak events supports the pulsed plant stress hypothesis in explaining WSB outbreak dynamics: High moisture stress is essential to feeding increases in WSB populations and dispersal rates, and a shift to low moisture stress is necessary to maintain the inflated outbreak populations.

As climate change causes greater climate variability, it should continue to affect WSB population dynamics. Projected changes in regional and global temperatures and precipitation over the next century will increase the likelihood of sustained drought conditions necessary for initiating WSB outbreaks. It’s also possible that the increase in drought conditions could hamper WSB outbreaks if drought conditions are sustained over too many consecutive years, or occur too frequently, since the climatic reversal to consecutive cool-wet conditions appears necessary in sustaining outbreaking WSB populations. Changes to land-use practices over the next century should also impact the occurrence of WSB outbreaks. A potential increase in forest fire occurrences with a changing climate could lead to changes in regional biomass available to WSB populations, leading to indirect effects on WSB dynamics (Flower et al. 2014b). Additionally, changing climate may drive shift the distribution of the WSB’s host populations over coming centuries. The results of our study suggests a complex combination of climate change, land-use patterns, and disturbances such as fires will continue affecting WSB outbreak dynamics in coming centuries, and continued study is needed to better understand how this complex interplay of exogenous factors will direct WSB populations.
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6. FIGURES AND TABLES

Table 1

Site and chronology characteristics for our four host sites and three non-host sites. The start of
the used record reflects either the common period shared by host and non-host trees, or the oldest
date with two or host more trees reporting.

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Elevation (m)</th>
<th># of trees</th>
<th>Oldest record</th>
<th>EPS (Pearson)</th>
<th>Interseries r (Pearson)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MPD</td>
<td>48.786</td>
<td>-119.243</td>
<td>1359</td>
<td>16</td>
<td>1685</td>
<td>0.933</td>
<td>0.686</td>
</tr>
<tr>
<td>SMD</td>
<td>48.561</td>
<td>-119.172</td>
<td>1379</td>
<td>18</td>
<td>1796</td>
<td>0.943</td>
<td>0.780</td>
</tr>
<tr>
<td>TMD</td>
<td>48.552</td>
<td>-119.225</td>
<td>1599</td>
<td>20</td>
<td>1685</td>
<td>0.936</td>
<td>0.650</td>
</tr>
<tr>
<td>VLD</td>
<td>48.825</td>
<td>-118.927</td>
<td>1286</td>
<td>15</td>
<td>1719</td>
<td>0.965</td>
<td>0.760</td>
</tr>
<tr>
<td>DCP</td>
<td>48.528</td>
<td>-119.029</td>
<td>1003</td>
<td>17</td>
<td>1685</td>
<td>0.942</td>
<td>0.627</td>
</tr>
<tr>
<td>TLP</td>
<td>48.672</td>
<td>-118.981</td>
<td>1334</td>
<td>6</td>
<td>1685</td>
<td>0.847</td>
<td>0.720</td>
</tr>
<tr>
<td>VLP</td>
<td>48.824</td>
<td>-118.927</td>
<td>1274</td>
<td>9</td>
<td>1685</td>
<td>0.936</td>
<td>0.760</td>
</tr>
</tbody>
</table>
Table 2

Cross-correlation (Pearson’s $r$; $p < 0.05$ except where noted) values of host chronologies and the regional non-host chronology against reconstructed (1685-2003) and historical (1895-2014) climate data. Positive correlation values with precipitation variables and negative correlation values with temperature variables support water stress being an important factor in radial growth.

<table>
<thead>
<tr>
<th>Site</th>
<th>PDSI (Cook)</th>
<th>PDSI (NOAA)</th>
<th>Previous year’s WYP</th>
<th>Previous year’s GYT</th>
<th>Mean July temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>MPD</td>
<td>0.49</td>
<td>0.54</td>
<td>0.42</td>
<td>-0.20</td>
<td>-0.20</td>
</tr>
<tr>
<td>SMD</td>
<td>0.55</td>
<td>0.59</td>
<td>0.45</td>
<td>-0.20</td>
<td>-0.14$^c$</td>
</tr>
<tr>
<td>TMD</td>
<td>0.37</td>
<td>0.39</td>
<td>0.28</td>
<td>-0.11$^c$</td>
<td>-0.18</td>
</tr>
<tr>
<td>VLD</td>
<td>0.51</td>
<td>0.57</td>
<td>0.42</td>
<td>-0.21</td>
<td>-0.15$^c$</td>
</tr>
<tr>
<td>Regional non-host</td>
<td>0.60</td>
<td>0.60</td>
<td>0.50</td>
<td>-0.20</td>
<td>-0.15$^c$</td>
</tr>
</tbody>
</table>

$^a$ Water-year (April to September) precipitation.

$^b$ Growing-year (previous October to current September) temperature.

$^c$ Value does not represent a significant ($p < 0.05$) relationship.
Table 3

Outbreak statistics for our four host sites. Mean return length represents the average period of time between outbreak cessations and subsequent outbreak initiations.

<table>
<thead>
<tr>
<th>Site</th>
<th># of outbreaks</th>
<th>Mean outbreak length</th>
<th>Mean return length</th>
<th>% of record outbreaking</th>
<th>Kruskal-Wallis chi-square*</th>
</tr>
</thead>
<tbody>
<tr>
<td>MPD</td>
<td>15</td>
<td>8.6</td>
<td>14.5</td>
<td>38.2</td>
<td>97.85</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*p &lt; 0.01</td>
</tr>
<tr>
<td>SMD</td>
<td>8</td>
<td>9.1</td>
<td>20.0</td>
<td>32.4</td>
<td>67.24</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*p &lt; 0.01</td>
</tr>
<tr>
<td>TMD</td>
<td>17</td>
<td>8.9</td>
<td>11.4</td>
<td>44.6</td>
<td>109.85</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*p &lt; 0.01</td>
</tr>
<tr>
<td>VLD</td>
<td>11</td>
<td>10.7</td>
<td>16.0</td>
<td>38.2</td>
<td>83.67</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*p &lt; 0.01</td>
</tr>
<tr>
<td>Regional</td>
<td>16</td>
<td>9.2</td>
<td>14.6</td>
<td>39.4</td>
<td>112.24</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*p &lt; 0.01</td>
</tr>
</tbody>
</table>

* Kruskal-Wallis ANOVA conducted on corrected indices during outbreak conditions against non-outbreak conditions.
Table 4

Percent of outbreak-only years occurring in the early (1685–1869) and modern (1870–2014) periods. Percents shown are the total number of years within each period’s length. Each of our four sites are represented, as well as the regional outbreak history with at least two sites reporting outbreaks concurrently. SMD (1796–2014) and VLD (1719–2014) do not represent equal measures of time between early and modern periods.

<table>
<thead>
<tr>
<th>Site</th>
<th>Moderate</th>
<th></th>
<th></th>
<th>Very high</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early</td>
<td>Late</td>
<td>Early</td>
<td>Late</td>
<td>Early</td>
<td>Late</td>
</tr>
<tr>
<td>MPD</td>
<td>34.1</td>
<td>43.4</td>
<td>21.6</td>
<td>23.4</td>
<td>5.9</td>
<td>14.5</td>
</tr>
<tr>
<td>SMD</td>
<td>20.3</td>
<td>38.6</td>
<td>8.1</td>
<td>22.1</td>
<td>0.0</td>
<td>6.9</td>
</tr>
<tr>
<td>TMD</td>
<td>41.6</td>
<td>48.3</td>
<td>6.5</td>
<td>26.9</td>
<td>2.2</td>
<td>11.7</td>
</tr>
<tr>
<td>VLD</td>
<td>33.8</td>
<td>42.8</td>
<td>13.9</td>
<td>22.1</td>
<td>2.6</td>
<td>13.1</td>
</tr>
<tr>
<td>Regional</td>
<td>30.8</td>
<td>50.3</td>
<td>9.7</td>
<td>28.3</td>
<td>0.0</td>
<td>14.5</td>
</tr>
</tbody>
</table>
Table 5

Paired, two-sampled t-test results for tested differences between PDSI values occurring during different outbreak conditions, including during outbreaks, between outbreaks, and in the two years immediately preceding outbreak initiations. Regional outbreak records (i.e., two or more sites outbreaks) were used to group PDSI data.

<table>
<thead>
<tr>
<th>PDSI variables</th>
<th>t-statistic</th>
<th>p-value</th>
<th>Mean of 1\textsuperscript{st} variable</th>
<th>Mean of 2\textsuperscript{nd} variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>During (1\textsuperscript{st}) &amp; between (2\textsuperscript{nd})</td>
<td>2.83</td>
<td>0.01</td>
<td>0.51</td>
<td>-0.26</td>
</tr>
<tr>
<td>outbreaks</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Two years prior to (1\textsuperscript{st}) and during (2\textsuperscript{nd})</td>
<td>-1.97</td>
<td>0.06</td>
<td>-0.67</td>
<td>0.51</td>
</tr>
<tr>
<td>(2\textsuperscript{nd}) outbreaks</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Two years prior to (1\textsuperscript{st}) and between (2\textsuperscript{nd})</td>
<td>-0.99</td>
<td>0.33</td>
<td>-0.67</td>
<td>-0.26</td>
</tr>
<tr>
<td>(2\textsuperscript{nd}) outbreaks</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>During outbreaks with two years prior to initiation dates (1\textsuperscript{st}) and between outbreaks</td>
<td>2.36</td>
<td>0.02</td>
<td>0.32</td>
<td>-0.20</td>
</tr>
</tbody>
</table>
Fig. 1

Location of host and non-host sites within the Okanogan Highlands. Note that VLD and VLP share a site in the northeast. Significant local features include the highest peak, Mount Bonaparte, immediately east of site MPD, and the Aeneas Valley dividing our southern sites from our northern locations. Service layer credits: ESRI, HERE, DeLorme, Mapmyindia, OpenStreetMap.
Fig. 2

Percent of trees recording an outbreak at our four host sites. The shifting black lines represents an 8-year moving average of percent of trees recording outbreak records, and the dashed line represents the unfiltered outbreak records. Two dotted straight lines indicate noted severity.
levels: 40% and 80% of trees at the site recording an outbreak.
Fig. 3
Modified Ripley’s K-function for moderate outbreak initiation dates and cessation dates. All dates were taken from our three sites dating to 1719 to include as much of the record with as many of our sites as we could. Y-axis represents a level of synchrony (positive) or asynchrony (negative) calculated using the temporal window (one to 30 years) shown on the X-axis, with the shaded region representing the confidence interval (95%). Any points outside the shaded region represent significant years in which synchrony occurs bidirectionally from outbreak years. Initiation and cessation dates report synchrony up to six and nine years, respectively.
Fig. 4

Modified Ripley's K-function calculated for all outbreak years (1719–2014) with moderate (40%) outbreak intensity. The top image represents all years of data. The middle and bottom images separate the outbreak years between early (1719-1869) and late (1870-2014) periods. Up
to 11 years of synchrony is recorded in all outbreak years. The early period shows up to three years of synchrony, while the late period shows up to nine years of synchrony.
Modified Ripley's K-function calculated for all outbreak years (1719–2014) with high (60%) outbreak intensity. The complete outbreak record reports synchrony up to 19 years. No significant synchrony is seen in the early period, while the late period outbreaks report up to nine
years of synchrony.
Fig. 6

Modified Ripley's K-function calculated for all outbreak years (1719–2014) with very high (80%) outbreak intensity. Note the change to the y-axis due to the decreased sample sizes for high-intensity outbreaks. The complete record shows significant synchrony of up to 26 years. No
synchrony existed in the early period’s very high intensity outbreaks. All synchrony was clustered in the late period, occurring up to 24 years.
Fig. 7
Superposed epoch analysis summary of our four sites' initiation and cessation dates using Cook et al.'s (1999; 2003) PDSI reconstructions. Instances of high significance are noted by dark grey
(90%) and black (95%) shading.
Fig. 8
Superposed epoch analysis using the regional outbreak initiation and cessation dates (i.e., at least two sites with concurrent outbreak conditions between 1685 and 2014).
Summary of superposed epoch analyses with historical (1895–2014) PDSI records and all four sites' initiation and cessation dates.
Fig. 10

Superposed epoch analysis using historical (1895–2014) PDSI records with regional outbreak initiation and cessation dates.