Drought-triggered western spruce budworm outbreaks in the interior Pacific Northwest: A multi-century dendrochronological record

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ABSTRACT

Douglas-fir forests in the interior Pacific Northwest are subject to sporadic outbreaks of the western spruce budworm, a species widely recognized as the most destructive defoliator in western North America. Outbreaks of the western spruce budworm often occur synchronously over broad regions and lead to widespread loss of leaf area and decrease in growth rates in affected stands. In spite of the ecological and economic significance of this defoliator, the mechanisms controlling this species' population dynamics are still not fully understood. We used dendrochronological methods to reconstruct three centuries of western spruce budworm outbreaks at thirteen sites along a transect running from central Oregon to western Montana and compared the outbreak reconstructions with regional drought history. The reconstructions reveal repeated western spruce budworm outbreaks that sometimes persisted more than a decade and were significantly synchronous among sites. Synchrony was higher in the second half of the record, possibly due to changes in forest composition and structure brought about by land use practices. Across stands and regions, there was a moderately strong relationship between initiation of synchronous outbreaks and periods of transitional climate conditions in which moisture availability was below average prior to outbreak initiation, but above average in the first few years of an outbreak. There was a weak relationship between cessation of outbreaks and one or more years of high moisture availability. Outbreaks tended to occur near the end of droughts. The association between climatic variability and outbreak dynamics observed across this transect indicates that climate is an important driver of western spruce budworm outbreaks. Other factors that we did not test, but that may influence outbreak dynamics include stand structure, forest composition, predation, and phenological synchrony between larvae and host trees. Future changes in western spruce budworm outbreak dynamics will be determined by a combination of changing climate, interactions with other disturbance agents, and changing forest composition and structure. Our results suggest that western spruce budworm outbreaks will likely intensify if drought frequency increases in the future.

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1. Introduction

Outbreaks of phytophagous insects are important drivers of forest dynamics through their effects on primary productivity, nutrient cycling, and succession. In the mixed-conifer forests of the interior Pacific Northwest, the dominant defoliating insect species is the western spruce budworm (*Choristoneura occidentalis* Freeman; Fellin and Dewey, 1982; Wickman, 1992). The larvae of this species feed primarily on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) trees. Defoliation by the western spruce budworm leads to reduced growth rates and mortality of limbs or entire trees (Alfaro et al., 1982; Ferrell and Scharpf, 1982). Outbreaks of this insect may also predispose host trees to subsequent infestations by other insects and pathogens (Alfaro et al., 1982; Ferrell and Scharpf, 1982; Hadley and Veblen, 1993). Outbreaks often extend over multiple states and may continue for well over a decade (Swetnam, 1986; Swetnam and Lynch, 1989, 1993; Swetnam et al., 1995; Ryerson et al., 2003). In 1986, at the peak of its last major outbreak, western spruce budworm affected more than 5.2 million hectares in the United States (Hofacker et al., 1987). Resurgence in the total area defoliated by the western spruce budworm starting in 2009 indicates that a widespread outbreak may be occurring for the first

time since the 1980s (Man, 2012). In spite of the ecological and economic significance of this species, its outbreak patterns, population dynamics, and responses to climatic variability are not fully understood.

Western spruce budworm populations often fluctuate synchronously over broad spatial scales, but the causal mechanisms of this synchrony are not fully understood (Peltonen et al., 2002). Analysis of synchrony patterns can offer insights into the mechanisms driving disturbance patterns over broad spatial scales and aid in predicting and responding to future disturbances. Synchrony of western spruce budworm populations is usually attributed to rapid dispersal of adult moths, the influence of exogenous forces such as climatic variability (the Moran effect; Moran, 1953), or a combination of the two (Myers, 1998; Cooke et al., 2007).

Climatic fluctuations, particularly changes in moisture availability, have been suggested as an important driver of western spruce budworm outbreaks (Hard et al., 1980; Thomson et al., 1984; Campbell, 1993; Swetnam and Lynch, 1993; Ryerson et al., 2003). However, different methods of quantifying climatic influences have yielded inconsistent results. Several studies based on dendrochronological reconstructions of outbreak events have found that they tend to occur during periods of high moisture availability (Swetnam and Lynch, 1993; Ryerson et al., 2003). In contrast, studies of modern observed western spruce budworm outbreaks have generally reported a tendency for outbreaks to occur following periods of low moisture availability (Hard et al., 1980; Thomson et al., 1984; Campbell, 1993). These contradictory results reflect a broader uncertainty regarding the role of climate in triggering outbreaks of herbivorous insects. Three competing hypotheses have been used to explain observed patterns of moisture availability associated with insect outbreaks. According to the *plant stress hypothesis*, drought or other abiotic stressors can trigger insect outbreaks through an increase in the nutritional quality of foliage due to the concentration of nitrogen or other beneficial nutrients or chemical compounds (White, 1984; Mattson and Haack, 1987). Alternatively, the *plant vigor hypothesis* proposes that the quality and/or quantity of foliage improves when moisture levels are high, thus benefiting some herbivorous insects (Price, 1991). More recently, the potential importance of the temporal variability, rather than simply the magnitude, of moisture stress was highlighted in the *pulsed plant stress hypothesis* (Huberty and Denno, 2004; Mody et al., 2009). The pulsed plant stress hypothesis proposes that intermittent plant stress may be particularly conducive to herbivorous insect outbreaks (Huberty and Denno, 2004; Mody et al., 2009).

In addition to these climatic triggers of outbreak events, there is evidence that land-use changes following Euro-American settlement of western North America have increased the synchrony, as well as severity, duration, and/or frequency, of western spruce budworm outbreaks in many ecosystems (Anderson et al., 1987; Swetnam and Lynch, 1989, 1993; Swetnam et al., 1995). Fire exclusion, logging, and grazing have increased the extent and homogeneity of densely stocked forests composed of tree species favored by the western spruce budworm (Hessburg et al., 1994; Keane et al., 2002). Additionally, the dense, multi-layered forest structure made common by the increase in shade-tolerant saplings makes stands especially vulnerable to western spruce budworm outbreaks, as this structure enables larvae to disperse downwards through the canopy layers with a low risk of falling to the forest floor where they would be more likely to be killed by predators (Maclauchlan and Brooks, 2009).

The relative importance of climatic variability, dispersal, and land-use practices on western spruce budworm dynamics cannot be known without long-term outbreak records covering pre- and post-settlement periods. Efforts to quantify and explain synchrony of western spruce budworm populations are hindered by short his-

torical records, which often only span the full length of a single major outbreak, and the limited geographic coverage of currently available dendrochronological reconstructions. The lack of long-term records has also limited efforts aimed at quantification of the relationship between climatic variability and outbreak dynamics. In this article, we present the results of a dendrochronological study in which three centuries of western spruce budworm outbreaks were reconstructed at sites along a transect running from central Oregon to western Montana. We use this multi-century record, along with observational records from the 20th century, to quantify the spatial synchrony of western spruce budworm outbreaks and to assess the association between moisture availability and the occurrence of outbreaks at multiple spatial scales. This is, to the extent of our knowledge, the first annually-resolved, multi-century analysis of the relationship between climate and the initiation and cessation of western spruce budworm outbreaks. Our analyses focus on answering the following questions:

(1) Over what temporal and spatial scales are western spruce budworm outbreaks synchronous?
(2) What is the relationship between moisture availability and the initiation, cessation, and synchronization of western spruce budworm outbreaks?

2. Materials and methods

2.1. Study area

Our thirteen sites are located along a 600 km longitudinal transect stretching from central Oregon to western Montana (Table 1; Fig. 1). The sites are located at middle elevations (1283–2040 m asl) in mixed-conifer stands dominated by a combination of Douglas-fir, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and/or grand fir. Some sites also have minor amounts of lodgepole pine (*Pinus contorta* Dougl. ex Loud.), western larch (*Larix occidentalis* Nutt.), western juniper (*Juniperus occidentalis* Hook.), or Rocky Mountain juniper (*Juniperus scopulorum* Sarg.). We also collected samples from ponderosa pine trees (see discussion of outbreak reconstruction methods below) at 12 nearby monospecific sites. The study area has a continental climate characterized by cold winters and warm summers. According to climate division records from the US Historical Climatology Network (http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp; Oregon climate divisions 7 and 8, Idaho climate division 4, and Montana climate divisions 1 and 2) for the period from 1895 to 2010, the average January and July temperatures are −4.7 °C (range: −7.6 °C to −1.6 °C) and 18.2 °C (range: 17.3–18.9 °C), respectively, and the average annual precipitation is 46.1 cm (range: 39.2–67.4 cm).

2.2. Sampling strategy

We targeted specific sites based on the presence of relatively old Douglas-fir and grand fir ("host") trees, field evidence or archival records of historical western spruce budworm outbreaks, and, where possible, the absence of recent stand-replacing fires and logging or other anthropogenic disturbances. To identify past outbreaks, we compared ring-width series from "host" tree species, those favored by the western spruce budworm, with ring-width series from "non-host" tree species. We used ponderosa pine as our non-host species because it is rarely defoliated by the western spruce budworm (Fellin and Dewey, 1982) and because its radial growth response to climate is similar to that of the primary host tree species, Douglas-fir (Fritts, 1974; Campbell et al., 2006).

At each site, we collected samples from eighteen or more Douglas-fir and grand fir host trees with a diameter of at least 40 cm at breast height (1.4 m) by removing two cores at breast

Table 1
Reconstructed outbreak statistics. Quiescent period calculated as years between cessation and subsequent initiation of reconstructed outbreaks.

Site	Latitude	Longitude	Elevation (m)	Record length	# Of outbreaks	Outbreak length	Quiescent period length
OCH	44.445	−120.322	1700	1668–2010	15	10	13
WLF	44.342	−119.782	1755	1680–2010	11	8	22
DIX	44.583	−118.626	1660	1739–2009	8	13	19
SMW	44.250	−118.694	2040	1618–2009	15	12	13
BWS	45.147	−117.633	1550	1715–2010	12	10	15
IMN	45.115	−117.002	1385	1678–2009	9	15	23
EFF	45.389	−115.963	1670	1701–2010	11	11	15
SFS	44.874	−115.700	1283	1703–2009	12	10	12
SHC	45.747	−114.450	1603	1683–2009	12	12	13
HUG	45.594	−114.213	1955	1588–2009	15	12	13
BIG	45.561	−113.844	1678	1708–2009	10	14	15
EAH	46.667	−113.583	1837	1702–2009	12	13	12
BHR	45.821	−112.941	1930	1640–2010	16	12	10
		Average:	331 years		12	12	15
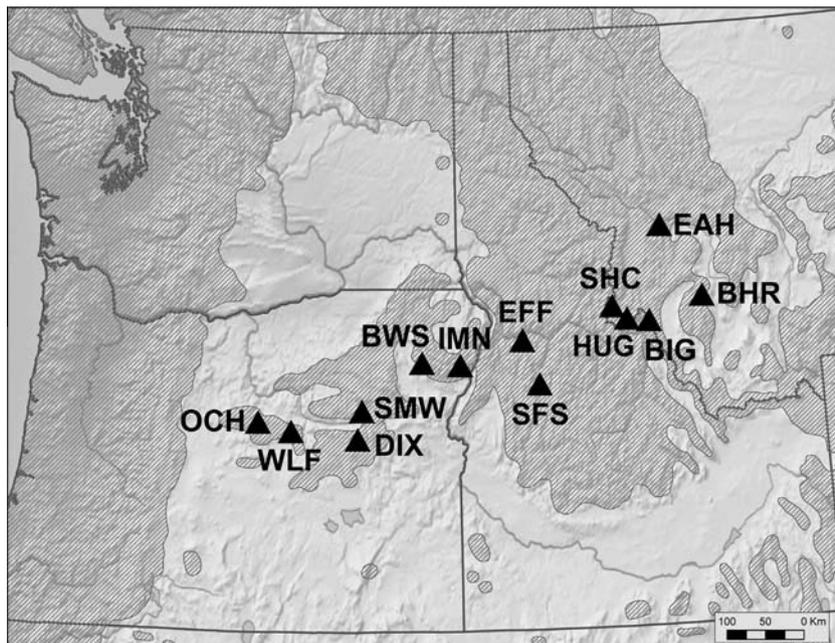
Fig. 1. Location of sites where we reconstructed western spruce budworm outbreak histories. Shaded area shows the distribution of Douglas-fir and grand fir (the primary host species for western spruce budworm), distribution data from Little (1971).

height using an increment borer. We selected these trees by sampling every host tree in a 120 × 8 m linear belt transect that roughly followed the slope contour. In addition, we opportunistically sampled the oldest-appearing host trees in a one hectare plot centered on the transect to ensure that the longest record possible was obtained.

Non-host sites were located in nearby stands that had few host-trees so as to avoid contamination of their climate signal by growth releases due to reduced competition caused by defoliation events. Twelve non-host sites were selected. At least 10 ponderosa pine trees were sampled at each non-host site to create a chronology that could be used to control for climate. Two cores were taken from each sampled tree at breast height using an increment borer.

2.3. Data preparation

We prepared core samples according to standard dendrochronological protocol (Stokes and Smiley, 1968) by air drying, gluing to slotted mounting boards, and sanding with progressively finer grades of sandpaper to enhance the visibility of the tree-ring boundaries. Ring-widths were measured to the nearest 0.005 mm with the aid of a microscope and a Velmex tree-ring measurement system. Visual crossdating, in which comparison of ring widths among samples is used to match characteristic patterns of width variations, was undertaken to ensure that each annual ring was dated to the correct calendar year (Stokes and Smiley, 1968; Fritts, 1976). Visual crossdating was statistically verified for all samples using the International Tree-Ring Data Bank software program COFECHA (Holmes, 1983).

The radial growth-rate of trees typically decreases as trees age, leading to a pattern of wider rings near the pith with increasingly narrow rings near the bark. This growth pattern creates an age-dependent growth trend in ring-width series that we removed through the process of standardization to create what is termed a ring-width index (Cook, 1985). The host and non-host ring-width indices used in this analysis were standardized using a 100-year cubic smoothing spline with a 50% frequency response, which retains most or all of the variability at annual to decadal time scales (Cook, 1985). Because western spruce budworm populations are known to fluctuate over decadal time scales (Swetnam and Lynch, 1993; Campbell et al., 2006), we chose this conservative standardization approach to retain variability at the relevant time scales.

To isolate the defoliation signal in our host ring-width indices, we developed a control index for each host site using only ponderosa

pine samples. The control indices were created by combining multiple prewhitened non-host chronologies via principal components analysis. First, we removed autocorrelation from our non-host ring-width series using an auto regressive moving average (ARMA) model to reduce non-climatic noise and meet the assumptions of several statistical tests used later in this study. The ARMA model for each individual standardized ring-width index was of an order determined by Akaike's Information Criterion (Cook, 1985). Next, the resulting time series from all non-host trees at a site were averaged to create a single master chronology for each site. We then used an unrotated principal components analysis to combine the non-host master chronologies from multiple nearby sites. For each host site, we selected three to five non-host chronologies based on the relative strength of their correlation with the host ring-width indices. We used the first principal component extracted from each set of non-host chronologies as a control chronology. Ten distinct control chronologies were produced, one of which was used at two host sites and one of which was used at three host sites. The first principal components explained 69–80% of the variance in the original chronologies and in every case were more strongly correlated with local climate records than individual chronologies or averages of multiple chronologies.

2.4. Outbreak reconstructions

Comparison of host and non-host ring-width series was used to remove the climate signal contained in the ring-width series, thereby isolating the outbreak signal. A "corrected" index was created by rescaling and subtracting the local non-host control index from the ring-width index of each individual host tree (Nash et al., 1975; Swetnam et al., 1985) using the following equation:

$$\text{Corrected Index} = I_{\text{host; year t}} - ((SD_{\text{host}}/SD_{\text{control}})$$
$$* (I_{\text{control; year t}} - \bar{I}_{\text{control}})) \tag{1}$$

where $I_{\text{host; year t}}$ is the ring-width index of an individual host tree in year t (the simple average of the standardized ring-width indices from the two cores taken from each tree), SD_{host} and SD_{control} are the standard deviations of the host ring-width index and non-host control index for the common period shared by both time series, $I_{\text{control; year t}}$ is the non-host control index in year t, $\bar{I}_{\text{control}}$ is the mean of the non-host control index for the common period. Positive values of this corrected index indicate growth above the level expected based on climate alone, while negative values indicate a growth reduction due to non-climatic factors (Nash et al., 1975).

We developed criteria for identifying outbreaks by carefully comparing our corrected indices with known periods of western spruce budworm outbreaks detected by the U.S. Department of Agriculture Forest Service during their annual aerial surveys (Williams and Birdsey, 2003; on file at the U.S. Department of Agriculture Forest Service offices of regions 1, 4, and 6). Our outbreak identification criteria detect long-lasting, relatively severe periods of growth reduction using a minimum growth-reduction duration and a minimum growth-reduction magnitude threshold. First, we identified periods of reduced growth during which no more than one consecutive year of positive corrected index values occurred. We allowed occasional, non-consecutive years of positive corrected index values because it is common for reduced growth to be interrupted by either temporary dips in western spruce budworm populations or brief, anomalous climatic events (Swetnam et al., 1995; Campbell et al., 2006). Second, we limited these periods of reduced growth to those persisting for four or more years, in order to separate western spruce budworm outbreaks from reductions caused by other forest insects, such as the Douglas-fir tussock moth, which have shorter outbreak cycles (Brubaker and Greene, 1979; Wickman et al., 1973; Swetnam et al., 1995). In spite of this, it is possible that a

Douglas-fir tussock moth outbreak immediately prior to or following a western spruce budworm outbreak could have been erroneously identified as part of a western spruce budworm outbreak (Swetnam et al., 1995). This minimum-duration criterion necessarily prohibited the identification of any short (<4 year) western spruce budworm outbreaks that may have occurred. Our analysis is therefore focused on sustained outbreak periods. Third, we limited these periods of four or more years to those when growth was at least 1.28 standard deviations below the long-term mean during one or more years (i.e., one year in each outbreak should be in the lowest 10% of corrected index values; Swetnam et al., 1985). Although admittedly somewhat arbitrary, this threshold has been widely used to identify outbreaks of western spruce budworm from tree rings in this and other regions (Campbell et al., 2006; Ryerson et al., 2003; Swetnam and Lynch, 1993; Swetnam et al., 1995).

Stand-wide outbreaks were defined as periods during which at least 40% of the host trees recorded an outbreak for four or more consecutive years. Alternative "percent of trees infested" thresholds were considered, but a 40%-or-more criterion was selected because this threshold resulted in outbreak periods that corresponded the closest to the outbreaks observed in the aerial surveys. We compared our reconstructed stand-wide outbreaks with outbreaks recorded at our sites in aerial survey data for the years 1977–1992 (the period covering the last major outbreak). Outbreaks were observed in aerial surveys at ten sites during this period. At these ten sites, the median percentage of years in which the observed and reconstructed records agree increases from 63% using a 30% threshold to 72% using a 40% threshold, and declines slightly to 69% using a 50% threshold. The disagreement between our reconstructed records and aerial survey records may be due in part to lags inherent in the radial-growth response of trees to defoliation. Lags of 1–3 years have been reported between the onset of defoliation and the onset of noticeable radial growth reductions and between the cessation of defoliation and the resumption of normal radial growth (Swetnam et al., 1995; Mason et al., 1997). Errors in the aerial survey data are also likely responsible for part of the disagreement. Aerial survey-based detection of outbreaks (Bennett and Tkacz, 2008) involves qualitative, subjective decisions and is prone to errors of both commission and omission (Johnson and Ross, 2008). For instance, Johnson and Ross (2008) reported that accuracy of detection of bark beetle outbreaks, which are generally more visible and easily detected than defoliator outbreaks, was only 61% using common aerial survey techniques.

We defined regionally synchronous outbreaks as periods of two or more years during which seven or more sites (i.e., over half the sites) simultaneously recorded a western spruce budworm outbreak. Additionally, we required that a regional outbreak include at least one site west of the Rocky Mountains (in northeastern Oregon or western Idaho) and at least one site in the Rocky Mountains (in eastern Idaho or western Montana).

Some of our analyses require outbreak initiation or cessation dates. We defined outbreak initiation as the first of at least two consecutive years in which an outbreak (either stand- or region-wide) was recorded, preceded by two or more years without an outbreak. The requirement for at least two years of non-outbreak conditions was chosen to remove "false-start" outbreak initiation dates that could occur after a one-year temporary decrease in the recorded level of infestation. We defined outbreak cessation as the first year of three or more years of non-outbreak conditions, so that cessation dates are the first year of non-outbreak conditions, rather the last year of outbreak conditions.

2.5. Statistical analysis of outbreak synchrony

We assessed regional synchrony of western spruce budworm outbreaks using three methods. This multi-method approach

allowed us to determine whether the proportion of trees experiencing an outbreak fluctuated synchronously among sites, quantify how this inter-site correlation among sites varied as a function of geographic distance, and assess whether discrete outbreak events occurred more closely clustered in time than would be expected based on chance. First, we assessed the temporal correlation among continuous time series of the percent of trees at each site indicating outbreak conditions during the 1739–2000 period common among all 13 sites using Pearson's correlation analysis. The high level of autocorrelation inherent to outbreak time series precludes a robust estimation of the statistical significance of the correlations among sites (Buonaccorsi et al., 2001). In spite of this limitation, the Pearson's correlation coefficients themselves still provide a basic measure of the relative strength of the relationship between specific site pairs (Buonaccorsi et al., 2001).

Second, we assessed the strength of spatial synchrony as a function of distance between sites by analyzing spatial autocorrelation in the time series of the percent of trees recording a western spruce budworm outbreak using Bjørnstad and Falck's (2001) nonparametric covariance function (NCF). The R (R Core Team, 2013) package NCF was used to produce continuous estimates of the nonparametric covariance function with smoothing splines. The NCF package also calculated bootstrapped confidence envelopes (based on 1000 iterations) for the covariance function estimates. The NCF uses a spline to produce a continuous estimate of fluctuations in the covariance among sites separated by increasingly large distances. In the resulting NCF graph, inter-site distances at which both the NCF curve and its confidence envelope are above (below) zero can be interpreted as a pattern of statistically significant positive (negative) covariance. This technique allowed us to visualize and assess variability in the covariance among outbreak records as function of the distance among sites, thus providing insight into the spatial patterns of synchronous population fluctuations.

Third, we determined whether discrete outbreak events were independent with respect to each other over a wide range of temporal lags using a modified one-dimensional Ripley's K-function (Ripley, 1976; Gavin et al., 2006; Bigler et al., 2007). This analysis tests for co-occurrence of outbreak years among any number of sites using increasingly long temporal search windows, and thus reveals the temporal scale of synchrony among many sites. Statistical significance was assessed using 1000 randomized simulations in which the records were shifted in a circular fashion by adding a random number of years to each record, rather than each year being individually randomized, in order to maintain the multi-decadal temporal patterns of outbreak dynamics in the randomized data. We implemented this analysis using records from all thirteen sites in K1D v1.2 (Gavin et al., 2006) for the 1739–2000 common period. Results were transformed to the L function for ease of interpretation. "Lhat" values above zero indicate synchrony, while values below zero indicate asynchrony and values near zero indicate independence of the records being compared. Because western spruce budworm outbreaks can last for several decades, we assessed a multi-decadal window for synchrony. Values were calculated over the span of temporal windows that varied from 0 years (i.e., synchrony during the year of event) to 50 years.

2.6. Statistical analysis of climatic influences on outbreak dynamics

We identified the climatic conditions associated with western spruce budworm outbreak initiation and cessation using superposed epoch analysis (Grissino-Mayer, 2001) at both stand and regional scales. This technique creates a composite of the climatic conditions associated with events by averaging the chosen climatic variable for years preceding and following each event (outbreak initiation or cessation). We conducted this analysis using both modern (1895–2010) and reconstructed (1575–2003) summer

(June, July, and August) Palmer Drought Severity Index records (PDSI; Palmer, 1965). The PDSI is a measure of moisture stress calculated using a combination of temperature, precipitation, and soil type data (Palmer, 1965). Both PDSI datasets provide records of moisture availability that are independent of the chronologies used to identify outbreak periods.

To explore climate-outbreak relationships over long time scales, we obtained multi-century records of PDSI from Cook et al.'s (1999, 2004) gridded dendroclimatological reconstruction. We used the neighboring (i.e., one of the four closest) PDSI grid cell(s) most highly correlated (Pearson's) with the ring-width time series at each of our sites. For sites located near the border of multiple grid cells, we averaged the PDSI time series from the neighboring grid cells when they were equally highly correlated with the ring-width series from that site. To satisfy the assumptions of superposed epoch analysis, we removed temporal autocorrelation from the PDSI time series using an ARMA model of an order determined based on Akaike's Information Criterion. At each site, we computed departures of climate in an 11-year window: the outbreak initiation date and the 5 years preceding and following outbreak initiation. We assessed the statistical significance of the climate departures by bootstrapping confidence intervals from 1000 Monte Carlo simulations (Mooney et al., 1993). Each Monte Carlo simulation involved randomly permuting the outbreak dates within the time period of analysis. Confidence envelopes for each lag year were determined from the 2.5th and 97.5th percentiles on the distribution of simulated results separately at each site. This analysis was repeated using outbreak cessation, rather than initiation, dates for each site. Identical analyses were undertaken for the initiation and cessation dates of widespread, regionally synchronous outbreaks.

To compare outbreak events with instrumental, rather than tree-ring reconstructed, records of climate, we also completed a superposed epoch analysis for 20th century outbreak initiation and cessation dates using instrumental records of climate division PDSI. Monthly climate division PDSI time series for our study region were obtained from the National Climatic Data Center for the period from 1895 to 2010. Monthly records of June, July, and August PDSI were averaged to create a record of summer moisture stress that was directly comparable to our reconstructed record of PDSI.

3. Results

3.1. Outbreak reconstructions

The thirteen outbreak reconstructions have starting dates between 1588 and 1739 (Fig. 2; Table 1). During the 1739–2000 common period, we reconstructed an average of 12 separate outbreaks per site (range 8–16). Outbreak durations varied widely (4–40 years) but the average duration was fairly consistent among sites (12 years, range 8–15 years per site). An average of 15 years elapsed between outbreaks. This quiescent period was more variable than the number and duration of outbreaks, with a range from 3 to 61 years. The average quiescent period varied from 10 years at BHR to 23 years at IMN.

3.2. Inter-site outbreak synchrony

Visual assessment of the outbreak reconstructions from different sites (Fig. 2) reveals a pattern of synchronous peaks and troughs in the number of infested trees. Summing the annual number of sites recording an outbreak (Fig. 3) shows clear clustering of outbreak dates, with 75% or more of the sites recording the same conditions (either outbreak or not outbreak) during 89 (34%) of the 261 years in the common period (1739–2000) and 66% or more of the sites recording the same conditions during 148 individual
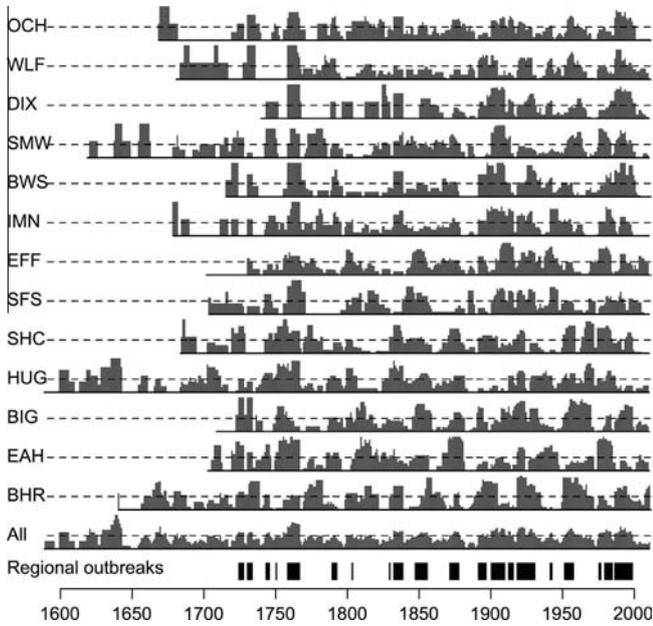
Fig. 2. Outbreak records as percent of trees recording an infestation at each site. Bottom plot is the percent of all trees at all sites recording an infestation. Solid line at base of each site's record indicates the total record length, defined as the period in which data were available from at least two trees. Dashed line indicates the 40% threshold used to identify outbreak periods. Black bars on bottom row show years in which widespread, regional outbreak conditions occurred (i.e., 7+ sites recorded an outbreak).

years (57%) of the common period. We identified 17 regionally synchronous (i.e., occurring in more than half of the sites) outbreaks during 105 of the years during the common period (1739–2000). Region-wide outbreaks became more common during the second half of the record, with 70 of the 105 widespread outbreak years (67%) occurring between 1870 and 2000.

Pearson's correlations among time series of the percent of trees recording an outbreak at each site confirmed the tendency towards synchronous western spruce budworm outbreak dynamics among sites and highlighted patterns of enhanced synchrony within subsections of the transect. The average inter-site correlation across the entire transect was 0.3, suggesting a weak positive association among records of the percent of trees indicating outbreak conditions. The correlation was generally higher for adjacent sites, and tended to be higher among sites with a similar position relative to the Rocky Mountains. The average inter-site correlation (Pearson's r) was 0.46 among the seven sites west of the Rocky Mountains and 0.40 among the five sites in the Rocky Mountains. There was a weak trend towards increased synchrony of outbreaks after 1870. The average correlation among sites west of the Rocky
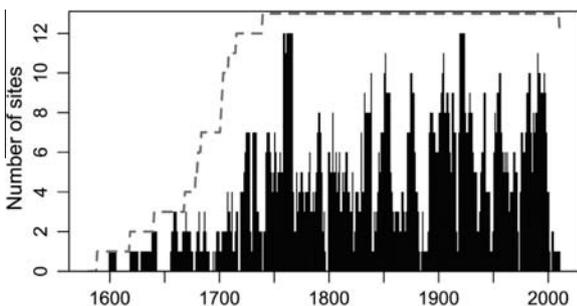

Fig. 3. Number of sites recording an outbreak (bars), and number of sites reporting (i.e., sample depth, dashed grey line).

Mountains increased from 0.44 during the first half of the common period to 0.47 during the second half. Similarly, the average correlation among sites in the Rocky Mountains increased from 0.38 during the first half of the common period to 0.42 during the second half.

Consistent with the above results, the nonparametric covariance function shows a gradual decrease in synchrony with increasing geographic distance (Fig. 4). The covariance of the western spruce budworm outbreak time series was higher than the region-wide average covariance at distances up to 205 km and statistically significantly higher than the region-wide average at distances <50 km.

The modified one-dimensional K-statistic calculated for all outbreak years at all sites shows a high and consistently statistically significant level of synchrony at temporal scales of up to 23-years (Fig. 5). When outbreak initiation dates and outbreak cessation dates were assessed for synchrony among sites, both showed statistically significant synchrony at temporal scales of up to 5 years
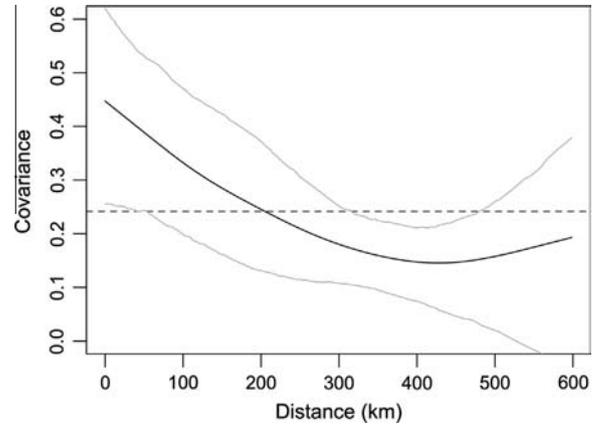
Fig. 4. Nonparametric covariance function (dark line) showing covariance among records of the percent of trees indicating outbreak conditions at all 13 sites as a function of distance between site pairs. Light grey lines are 95% confidence intervals for estimates of the nonparametric covariance function based on a smoothing spline. Dashed line shows the average region-wide covariance.
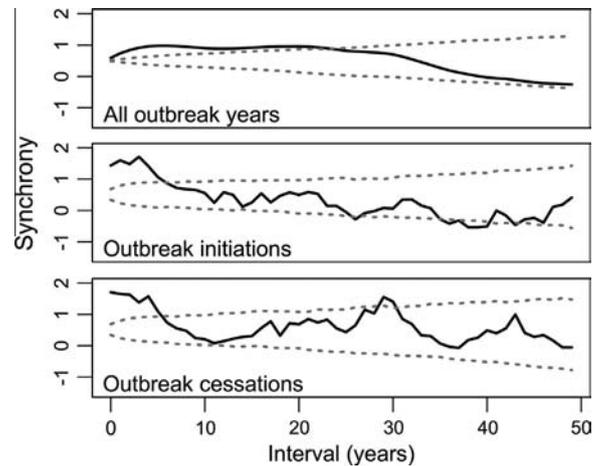
Fig. 5. Modified multivariate Ripley's K-function calculated for all outbreak years (top), outbreak initiation dates (center), and outbreak cessation dates (bottom) at all sites over the 1739–2000 common period. Y-axis shows L-function values (see text for explanation), which can be interpreted as an index of synchrony, with positive values indicating synchrony and negative values indicating asynchrony. Synchrony was assessed among all sites over multiple temporal windows, as shown on the X-axis. Light grey lines represent a 95% confidence interval based on randomizing the outbreak records relative to each other.

(Fig. 5). Due to the often gradual changes in western spruce bud-worm populations during outbreak initiations/cessations, it is not surprising that synchrony is detected at temporal scales of more than a single year.

3.3. Influence of climatic variability on outbreak timing and synchrony

At all 13 sites, outbreak initiation dates were preceded by up to three warm-dry years (Fig. 6). When viewing superposed epoch analysis results on a site-by-site basis (Fig. 7), nine of the sites experienced at least one year of statistically significant warm-dry negative PDSI departures during the four years preceding outbreak initiation. Outbreak initiation tended to be followed by relatively cool-wet conditions. Eight of the sites experienced statistically significant positive PDSI departures during at least one of the four years beginning with the year of outbreak initiation (Fig. 7). This tendency toward wetter conditions was most pronounced in the third year following outbreak initiation, during which 12 sites had positive PDSI anomalies, five of which were statistically significant.

Climate was generally cool-wet preceding outbreak cessation and warm-dry following outbreak cessation, although these departures were generally small and rarely statistically significant (Figs. 6 and 8). Climate at all 13 sites was relatively cool-wet during at least two of the three years preceding outbreak cessation and all sites were relatively warm-dry the year the outbreak ceased and/or the year after.

The relationship of outbreaks to climate during the 20th century, as assessed from climate-division data, was similar to that in prior centuries, as reconstructed from tree-ring data. There are few statistically significant results for the 20th century analysis, but this is likely due in part to the limited number (3–5 at each site) of outbreak initiations and cessations that occurred during the 20th century. Outbreak initiation dates during the 20th century tended to follow one to two years of below-average PDSI values (Fig. 9). Eleven of the 13 sites experienced at least one year of drought in the two years preceding outbreak initiation. No consistent pattern was apparent in the average PDSI values during the

year of and two years following outbreak initiations. However, 12 sites had a tendency towards wetter-than-average conditions in the third year following outbreak initiation. All 13 sites experienced above-average moisture availability during one to three years preceding outbreak cessation (Fig. 9).

Regionally synchronous outbreaks exhibited a relationship with climate that closely mirrored the results for outbreak initiation at individual sites. There was a significant tendency for warm-dry conditions to occur two years before outbreak initiation, and for cool-wet conditions to occur during the year of and three years after regionally synchronous outbreak initiation dates (Fig. 10).

4. Discussion

4.1. Outbreak histories

Our results reveal outbreak dynamics broadly similar to those in other regions. The mean outbreak duration (12 years) and mean length of quiescent periods between outbreaks (15 years) at our sites does not differ greatly from those reported in dendrochronological reconstructions in northern New Mexico (mean duration: 22 years, mean quiescent interval: 11 years; Swetnam and Lynch, 1993), northeastern Oregon (mean duration: 15 years, mean quiescent interval: 21 years; Swetnam et al., 1995), and southern British Columbia (mean duration: 12 years, mean quiescent interval: 29 years; Campbell et al., 2006).

4.2. Inter-site outbreak synchrony

Both visual assessment and statistical analysis of the outbreak reconstructions show that western spruce budworm populations at our sites have fluctuated synchronously over hundreds of kilometers during the past several centuries. The nonparametric covariance function results (Fig. 4) exhibit the gradual decrease in synchrony with increasing geographic distance typical of the outbreak dynamics of many insect species (Peltonen et al., 2002). We found that geographic distance is not the only factor controlling the level of spatial synchrony in outbreak dynamics. Our results revealed a pattern of higher synchrony among sites located in similar positions relative to the Rocky Mountains. This suggests that major topographic barriers, presumably through their influence on western spruce budworm dispersal and/or local climate, and differences in dominant climate patterns (i.e., the relative importance of continental vs maritime air masses) also appear to govern synchrony.

Synchrony of disjunct populations is often attributed to trophic interactions with other highly mobile predator or prey species, dispersal of individual organisms from areas of high population density to areas of low density, the Moran effect, or some combination of those factors. Moran (1953) proposed the concept, now known as the Moran effect, that variability of spatially autocorrelated exogenous abiotic factors, particularly those related to climate, could synchronize disjunct populations. Little is known about the dispersal capabilities of the western spruce budworm (Willhite and Stock, 1983; Campbell, 1993; Peterson and Denno, 1998). Female moths of other *Choristoneura* species are able to migrate over 100 km (Greenbank et al., 1980; Dobesberger et al., 1983; Peterson and Denno, 1998), but the dispersal abilities of the western spruce budworm are believed to be lower (Willhite and Stock, 1983). Genetic analyses indicate that dispersal may occur regularly among populations of the western spruce budworm within relatively small areas (between sites less than 350 km apart), but is far less common over larger spatial scales (Willhite and Stock, 1983). Peltonen et al. (2002) found no consistent relationship between dispersal capacity and synchrony of lepidopteran
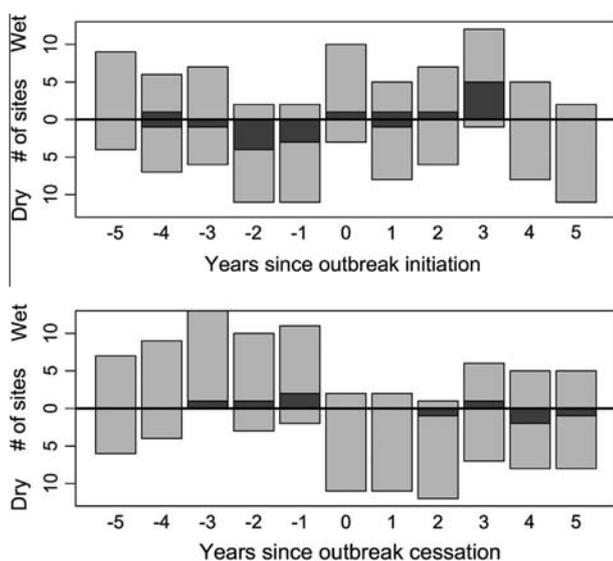
Fig. 6. Summary of superposed epoch analysis indicating the direction of reconstructed 1739–2000 Palmer Drought Severity anomalies (Cook et al.) for an 11-year window centered on outbreak initiation (top) and cessation (bottom) dates. Descending bars show the number of sites with a negative association with PDSI (i.e., droughty conditions), ascending bars show the number of sites with a positive association with PDSI (i.e., wetter conditions). Dark gray shading shows number of sites with statistically significant (at the 95% confidence interval) anomalies.
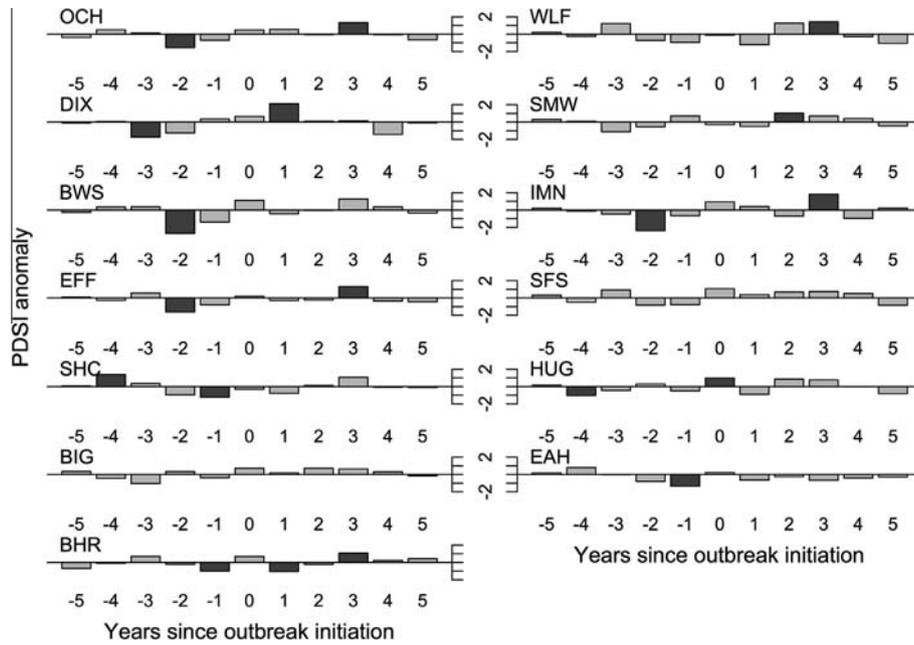
Fig. 7. Superposed epoch analysis indicating the direction of reconstructed 1739–2000 Palmer Drought Severity anomalies for an 11-year window centered on outbreak initiation dates at each of our 13 sites. Descending bars indicate a negative association with PDSI (i.e., droughty conditions), ascending bars indicate a positive association with PDSI (i.e., wetter conditions). Dark grey shading shows statistically significant (at the 95% confidence interval) anomalies.
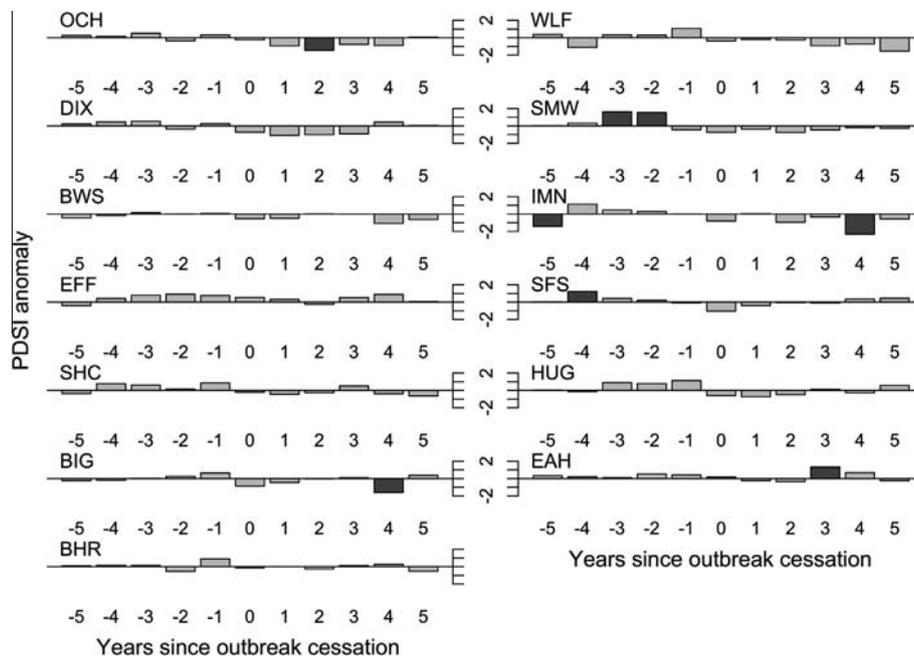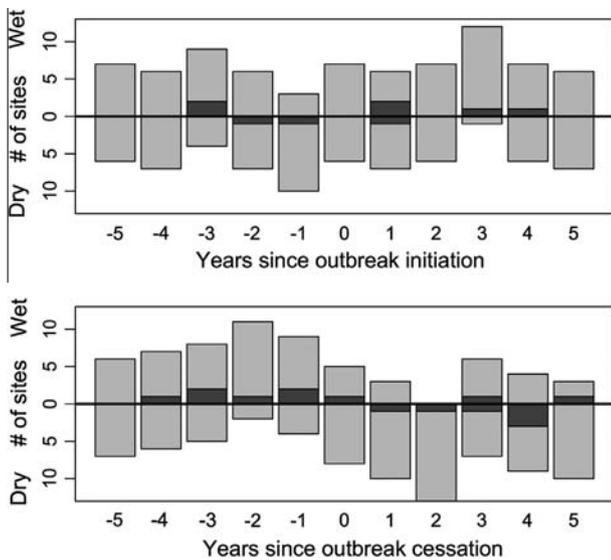

Fig. 8. Superposed epoch analysis indicating the direction of reconstructed 1739–2000 Palmer Drought Severity anomalies for an 11-year window centered on outbreak cessation dates at each of our 13 sites. Descending bars indicate a negative association with PDSI (i.e., droughty conditions), ascending bars indicate a positive association with PDSI (i.e., wetter conditions). Dark grey shading shows statistically significant (at the 95% confidence interval) anomalies.

defoliators during the late 20th century, and concluded that dispersal was not an important driver of synchrony for these species. At our sites, the lower synchrony among populations in different positions relative to the Rocky Mountains suggests that any role dispersal may play in synchronizing disjunct populations is limited by topographic barriers. Ultimately, the distinction between dispersal and the Moran effect may be less clear than often assumed, as weather conditions influence dispersal rates and patterns (Sanders et al., 1978; Royama, 1984). Our analysis revealed widespread associations between moisture stress and the timing of

both stand-level and regionally synchronous outbreaks. This suggests that climatic variability, which varies over similarly large spatial scales, is likely an important driver behind the observed pattern of synchronous outbreak dynamics.

We found that regional synchrony of western spruce budworm outbreaks was higher in the second half of our record. Similar increases in synchrony over the 20th century have been identified elsewhere (Swetnam and Lynch, 1989, 1993). This shift in outbreak dynamics may be due in part to the changing climatic conditions observed in the Pacific Northwest over the last 100+ years (Mote,

Fig. 9. Summary of superposed epoch analysis indicating the direction of climate-division Palmer Drought Severity anomalies for an 11-year window centered on 20th century (1900–2000) outbreak initiation (top) and cessation (bottom) dates. Descending bars show the number of sites with a negative association with PDSI (i.e., droughty conditions), ascending bars show the number of sites with a positive association with PDSI (i.e., wetter conditions). Dark gray shading shows number of sites with statistically significant (at the 95% confidence interval) anomalies.
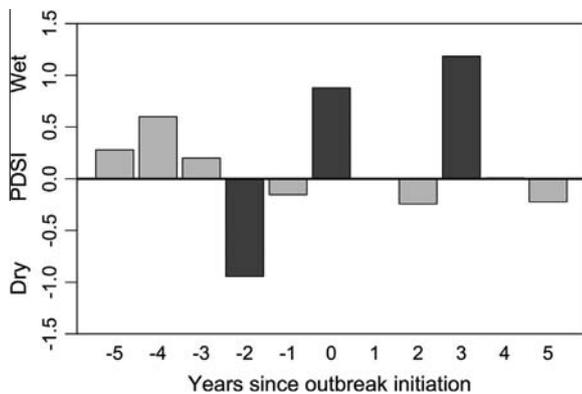
Fig. 10. Superposed epoch analysis results for the initiation of regionally synchronous outbreaks during the 1739–2000 common period. Palmer Drought Severity (PDSI) anomalies for an 11-year window centered on the first year of periods during which seven or more sites experienced synchronous outbreaks. Negative PDSI anomalies indicate droughty conditions. Dark grey shading indicates statistically significant (at the 95% confidence interval) anomalies.

2003). Increased synchrony is also likely partially attributable to changing land-use practices that have resulted in an increase in the extent and homogeneity of dense, multi-story forests of tree species favored by the western spruce budworm (Hessburg et al., 1994; Keane et al., 2002; Maclauchlan and Brooks, 2009).

4.3. Influence of climatic variability on outbreak timing

To the best of our knowledge, this study is the first explicit, detailed analysis of the relationship between climate and the specific initiation and cessation dates of western spruce budworm outbreaks over long (multi-century) time scales. We found that periods of transitional climate conditions were commonly associated with the initiation of western spruce budworm outbreaks, with warm-dry conditions occurring in the three years preceding outbreak initiation, and cool-wet conditions occurring during the

year of and three years following outbreak initiation. Thus, our results indicate that western spruce budworm outbreak initiations occurred most frequently during periods of transitional climatic conditions near the end of droughts. Climate may be a particularly important factor during the earliest stages of an outbreak, before populations have surpassed the threshold above which predators and host-tree defensive compounds are no longer strongly limiting (Campbell, 1993). Because one-to-three year lags have been reported between the onset of defoliation and the onset of noticeable radial growth reductions (Swetnam et al., 1995; Mason et al., 1997), preceding climate conditions during one-to-three years prior to reconstructed outbreak initiations may actually represent conditions during the earliest phase of the outbreak.

Our evidence does not entirely support either the plant stress hypothesis or the plant vigor hypothesis. Moisture stress appears to be an important precondition for outbreak initiation at our sites, as would be predicted by the plant stress hypothesis (White, 1984; Mattson and Haack, 1987). On the other hand, a transition to above-average moisture availability following outbreak initiation appears to be necessary for an initial population expansion to continue long enough to become an outbreak, which is more in line with the plant vigor hypothesis (Price, 1991).

The pattern of dry summer conditions preceding outbreaks has not been reported in previous dendrochronological studies. This difference is likely linked to the temporal scale being assessed. By focusing on annual values in the years surrounding outbreak initiation, rather than analyzing averages over the duration of an outbreak, we were able to identify common patterns of climatic conditions during a critical part of outbreak cycles. We also identified a prevalent pattern of cool-wet conditions in the three years following outbreak initiation, which is congruent with previous dendrochronological studies that have identified a pattern of cool/wet conditions during outbreaks (Swetnam and Lynch, 1993; Ryerson et al., 2003). This finding is further supported by Williams and Liebhold (1995), who found that 20th century outbreaks tended to occur more frequently in wetter areas of eastern Oregon.

The association we found between moderate-severity, short-duration drought and the initiation of western spruce budworm outbreaks is biologically reasonable based on modern observations of the climate drivers of such outbreaks. Twentieth century outbreaks of western spruce budworm are more frequent and of longer duration in forests with relatively dry climates (Wulf and Cates, 1987; Campbell, 1993; Maclauchlan et al., 2006; Maclauchlan and Brooks, 2009; Murdock et al., 2013) and low average soil moisture (Williams et al., 1971; Kemp and Moody, 1984). Furthermore, modern outbreak initiation tends to follow periods of warm and dry weather, particularly during the summer preceding outbreak initiation (Hard et al., 1980; Thomson et al., 1984; Campbell, 1993).

The survival and growth of western spruce budworm larvae is negatively correlated with dietary moisture content (Clancy, 1991), and larval survival, growth, and reproductive rates are greater during periods of low precipitation and/or available soil moisture (Cates et al., 1983; Mattson and Haack, 1987; Campbell, 1993; Parks, 1993). Moderate drought stress may favor western spruce budworm by increasing drought-stressed host trees' foliar concentration of sugars, nutrients (especially nitrogen), and favorable chemical compounds such as beta-pinene (Martinat, 1987; Mattson and Haack, 1987; Campbell, 1993; Parks, 1993). However, the relationship between larval survival and moisture may be non-linear as prolonged or severe drought conditions have been linked to reduced larval survival rates (Mattson and Haack, 1987; Campbell, 1993; Huberty and Denno, 2004). This non-linear relationship may explain why we found an association with drought prior to outbreak initiation and increased moisture following outbreak initiation. Additionally, higher moisture availability following

outbreak initiation would allow for increased needle production (Gower et al., 1992; Krause et al., 1993) and possibly reduced needle toughness (Krause et al., 1993), which could reduce the risk of starvation for western spruce budworm larvae during prolonged outbreak conditions. The pulsed plant stress hypothesis (Huberty and Denno, 2004; Mody et al., 2009), in which intermittent plant stress is described as particularly conducive to herbivorous insect outbreaks, therefore appears to be a better fit for our results than either the plant vigor hypothesis or the plant stress hypothesis.

Other climatic factors likely also play an important role in the timing of outbreak initiations. Windy conditions and heavy precipitation events can blow larvae out of their host trees (Campbell, 1993). Low temperatures in the late spring and early summer can kill larvae directly through freezing or indirectly by killing host tree foliage, thus leading to western spruce budworm starvation (Fellin and Schmidt, 1973; Wulf and Cates 1987). Early spring temperatures also play an important role in regulating the synchrony of larval emergence and host tree budburst, as the timing of both larval emergence and budburst are influenced by accumulation of degree days (Chen et al., 2003; Shepherd, 1983; Thomson and Benton, 2007; Thomson and Moncrieff, 1982). Mismatches between larval emergence and budburst lead to increased larval mortality as larvae that emerge too early or too late will be forced to disperse in search of suitable food, which increases the chances of encountering predators, or to eat suboptimal older needles to avoid starvation, which can hamper larval growth (Chen et al., 2003; Shepherd, 1983).

The relatively weak association we found between climate and the cessation of western spruce budworm outbreaks is not surprising, as cessation of defoliator outbreaks is often attributed to the increase in the defoliator population being outpaced by an increase in the population of their predators or to a loss of food caused by widespread, severe herbivory of the host species, rather than to climate (Cooke et al., 2007). However, the non-significant but widespread relationship revealed through superposed epoch analysis suggests that climate may in fact be an important component in outbreak cessation timing. Although years both preceding and following outbreak cessation showed a weak pattern of anomalies, the association with climate during preceding years may be interpreted more readily as causal. Because we defined outbreak cessation as the first year in which no outbreak conditions were detected, western spruce budworm populations must have declined very early in the summer or prior to that year. As with outbreak initiations, a one-three year lag between the cessation of defoliation and the resumption of normal radial growth has been reported in previous studies (Swetnam et al., 1995; Mason et al., 1997). Outbreak cessation dates therefore reflect prior environmental conditions linked to western spruce budworm population decline. Outbreak cessations tended to follow a period of several years with positive PDSI values. Prolonged above-average moisture availability may decrease larval survival and growth rates through changes in foliar chemistry, as discussed above. Additionally, if wet years are associated with cooler, stormier conditions during the late spring or early summer, this could conceivably reduce western spruce budworm populations by altering the timing of larval emergence relative to the timing of host trees' budburst (Shepherd, 1983; Campbell, 1993; Chen et al., 2003) and through direct mechanical damage to larvae during storms (Fellin and Dewey, 1982; Campbell, 1993).

5. Conclusion

Western spruce budworm outbreaks have occurred frequently over the last three centuries in the interior Pacific Northwest. Outbreaks sometimes persisted more than a decade and were significantly synchronous among sites. Synchrony was higher in the second half of the record, possibly due to changes in forest composition and structure brought about by land-use practices. Across stands and regions, there was a strong relationship between initiation of synchronous outbreaks and prior periods of low moisture availability followed by high moisture availability, while there was a weak relationship between cessation of outbreaks and one or more years of high moisture availability. Both local and regionally synchronous outbreaks tended to occur during periods of fluctuating climate conditions near the end of droughts. Our results indicate that the pulsed plant stress hypothesis is an appropriate conceptual model for the relationship between moisture availability and outbreaks of this species. The association between climatic variability and outbreak dynamics across the transect indicates that broad-scale climatic variability is an important driver of western spruce budworm outbreaks. Improved understanding of the influence of climatic variability on outbreak occurrence and regional synchrony should help forest managers anticipate future changes in outbreak patterns.

Our results show that western spruce budworm outbreak patterns have responded to climatic variability over the last three centuries and can be expected to undergo further changes in response to future climatic changes. Temperatures increased over the 20th century across the interior Pacific Northwest and further increases in temperature are projected for the 21st century (Mote and Salathé, 2010). Global climate model projections of changes in precipitation are more variable than those of temperature, but a decrease in summer precipitation also appears likely for this region (Mote and Salathé, 2010). Our results suggest that western spruce budworm outbreak activity is likely to increase over the coming century in response to a shift towards warmer, drier and more variable climatic conditions. This agrees with previous predictions of intensified western spruce budworm activity in many regions over the next century due to future climate change (Murdock et al., 2013). Increased frequency of drought could create improved conditions for the initiation and synchronization of western spruce budworm outbreaks if droughts are followed by a rapid reversal to above-average moisture availability. However, this effect would be tempered by the potential for increasing duration of droughts, as our results indicate that long-lasting droughts may inhibit western spruce budworm outbreaks. Increased drought occurrence may also lead to increases in the size or frequency of fires (Westerling et al., 2006; Krawchuk et al., 2009; Marlon et al., 2012), which could reduce the extent and density of mixed-conifer forests. Furthermore, over longer time scales climatic changes will also indirectly impact outbreak patterns via changes in the distribution of suitable host trees (Williams and Liebhold, 1995). Therefore, future changes in western spruce budworm outbreak dynamics will be determined by a combination of changing climate, interactions with other disturbance agents, and changing forest composition and structure.

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