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Characterization of Western Spruce Budworm Outbreak Regions in the British Columbia Interior

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Abstract

The western spruce budworm (*Choristoneura freemani* Razowski; WSB) shapes Douglas-fir (*Pseudotsuga menziesii*) (Mirb.) Franco forests throughout western North America with periodic, severe landscape-level defoliation events. The largest and most continuous recorded defoliation occurred in the 2000s, largely centered in the Williams Lake and 100 Mile House WSB Outbreak Regions, peaking in 2007 at 847,000 hectares defoliated in B.C. Unique WSB Outbreak Regions in south central B.C. are described using biogeoclimatic ecosystem classification, geography, 106 years of documented defoliation, and 46 stand-level Douglas-fir host tree-ring chronologies. Since the 1980s, recorded defoliation in B.C. has shifted from coastal ecosystems and become a dominant disturbance in drier, colder, Interior Douglas-fir ecosystems. Defoliation records demarcate four outbreaks from 1950-2012 and up to three growth suppression events from 1937-2012. Outbreak duration was shorter in the north and far south of B.C. with recovery periods (no trees showing growth suppression) shorter over all WSB Outbreak Regions in the 2000s, suggesting trees may be increasingly susceptible to each successive defoliation event. Knowing the regional outbreak periodicity may facilitate early detection of incipient WSB populations, which is critical for management as many of our low elevation Douglas-fir forests become more stressed with changing and unpredictable climate regimes.

Key Words: western spruce budworm, B.C. outbreak history, aerial overview records, dendrochronology, Douglas-fir

Introduction

The western spruce budworm, *Choristoneura freemani* Razowski, formerly *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae) (WSB), is a native defoliator that periodically experiences often long lasting, landscape level population outbreaks throughout its range in western North America (Fellin and Dewey 1982; Maclauchlan et al. 2006; Volney and Fleming 2007). WSB primarily feeds on both coastal (*P. menziesii* var. *glauca* (Beissn.) Franco and interior Douglas-fir (*Pseudotsugae menziesii* var. *menziesii* (Mirb.) Franco), but also feeds on true firs (*Abies* spp.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and western larch (*Larix occidentalis* Nutt.) (Furniss and Carolin 1977; Fellin and Dewey 1982; Fellin 1985). Cumulatively since 1909, approximately 3.5 million hectares of interior Douglas-fir forest have been defoliated (Table 1) one or more times by WSB in British Columbia (B.C.) (Parfett et al. 1994; FLNR 1996-2016; Maclauchlan et al. 2006). WSB is an early season defoliator that totally or partially consumes new buds and flushing foliage. This feeding pattern results in uneaten foliage, which dries and turns a characteristic reddish brown that is easily detected from the air and the ground. WSB survival, population growth, and subsequent impacts to the tree are closely tied to its synchrony with budflush and depend upon the tree's age, position in the canopy, and geographic location (elevation, latitude) (Swetnam and Lynch 1993; Maclauchlan and Brooks 2009; Nealis 2012). Outbreaks are a result of several influences and processes, including climate (Thomson et al. 1984; Campbell et al. 2006), reproduction, host availability, mortality factors and dispersal (Régnière 1982; Royama 1984; Régnière and Nealis 2007). Climate can promote more synchronized budflush and larval emergence, leading to an increase in reproduction and insect survival (Thomson 1979; Alfaro et al. 2014). This insect-host synchrony results in more complete bud destruction and defoliation by larvae. When viewed from a broad geographic scale, WSB exhibits expansive, sustained outbreaks; however, at a smaller geographic landscape scale, WSB may display rather fast-cycling, eruptive outbreaks (Campbell et al. 2005).

WSB can have devastating effects on Douglas-fir forests, by reducing overall growth and yield, increasing susceptibility to other insect pests and diseases, and limiting forest management options. Partial or selective harvesting may be compromised because WSB feeding will: reduce available seed source on affected sites; damage or kill understory trees that are relied upon as the next crop; and will increase the number of years until harvest cycle due to reduced radial growth (Alfaro and Maclauchlan 1992; Day 1996; Maclauchlan and Brooks 2009). Due to WSB's preferential feeding on the current year buds and foliage, height growth is severely reduced or eliminated during years of substantive defoliation. Feeding by this insect also causes stem defects, top-kill and tree mortality (Alfaro et al. 1982, 1985; Alfaro and Maclauchlan 1992) and is particularly damaging to understory and suppressed trees in multi-layered stands (Maclauchlan and Brooks 2009). The understory and suppressed component of stands have proportionally less new foliage and therefore fewer WSB larvae are needed to cause severe defoliation (Maclauchlan and Brooks 2009). The larger, overstory canopy trees can support much higher WSB densities (Magnussen et al. 2005) before defoliation causes significant top-kill or mortality (Alfaro et al. 1984; Alfaro 1986), or is even visible in aerial surveys. Defoliation also impedes the radial growth of trees by destroying photosynthetic tissue, thereby reducing the supply of carbohydrates needed for growth (Kramer and Kozlowski 1979). The width of annual rings produced during infestation years is reduced in response to the phenological synchrony of buds and larvae and the amount of larval feeding on foliage. This is characterized in the tree-rings as a cause–effect relationship that usually has a lag of one or more years (Alfaro et al. 1985; Alfaro and Maclauchlan 1992). After the infestation collapses, defoliated trees take several years to regain their full foliage compliment; during this period, radial-growth rates slowly recover.

Duration and periodicity of outbreaks may be changing in some geographic areas (Maclauchlan et al. 2006) as a response to global climate trends (Dale et al. 2001; Logan et al. 2003; Volney and Hirsch 2005; Battisti 2008), regional topography, host species composition, latitude, canopy structure and natural mortality factors. The most recent (1987-2015) WSB outbreak in B.C. extended north along the Fraser River to immediately south of Quesnel (Fig. 1), well beyond the previously recorded historical outbreak range (Maclauchlan et al. 2011). Early indications are that the impact in these more northern stands is more severe than in stands to the south (L. Maclauchlan, pers. observations). Stand composition and structure has changed dramatically over recent decades in more northerly stands located in the Cariboo-Chilcotin Plateau due to increased fire suppression and selective harvesting of larger, mature trees (Harvey et al. 2017). These practices have led to many stands developing dense, overstocked understory layers that are conducive to supporting high WSB populations (Maclauchlan and Brooks 2009). Also, in mixed-conifer stands, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has removed most of the lodgepole pine (*Pinus contorta* Dougl.) component (Westfall and Ebata 2008; Safranyik et al. 2010), leaving Douglas-fir- or spruce-dominated stands that offer a more susceptible resource for WSB. Interior Douglas-fir forests have seen a dramatic change in stand structure and composition over the last century, largely due to human interventions (Swetnam and Lynch 1993; Maclauchlan and Brooks 2009; Flower et al. 2014). Selective harvesting, fire exclusion and grazing in these forested ecosystems, coupled with climate change have promoted densely stocked, multi-layered forests favoured by WSB (Willhite and Stock 1983; Maclauchlan and Brooks 2009; Chen et al. 2010; Axelson et al. 2015; Senf et al. 2015).

Douglas-fir forests in the interior of B.C. occur predominantly in the Interior Douglas-fir (IDF) biogeoclimatic ecosystem classification (BEC) zone (Lloyd et al. 1990; Meidinger and Pojar 1991). All levels of B.C. government value the ecosystems of the IDF zone given the many overlapping resource values and social expectations. The forests of the IDF zone are challenging to manage due to social and ecological constraints. This zone encompasses a broad range of temperature and precipitation regimes, therefore often limiting harvest and regeneration options to single tree or group selection and natural regeneration (B.C. Ministry of Forests 1992; Day 1996). Providing a comprehensive characterization and understanding of WSB outbreak events in specific geographic areas throughout B.C. will inform management opportunities in susceptible forests. Just as stands in the IDF zone are complex in structure, density and stem size composition, so are the biology and natural cycling of WSB. Landscape and tree level data are used in this study to better understand WSB outbreak dynamics and impacts in B.C. The historic aerial overview survey data provide information on the geographic range, periodicity and duration of recorded WSB outbreaks. Data from tree cores provide information on the growth response of trees to episodes of WSB defoliation. The combination of these two spatial scales of analysis will provide a better understanding of future outbreak patterns and forest response.

In the current study, we incorporate numerous independent, but complementary, data sources to delineate and characterize unique WSB Outbreak Regions throughout the interior Douglas-fir forests of B.C. WSB outbreaks have been recorded in B.C. since 1909 (Harris et al. 1985; Alfaro et al. 2014), with more precise accounts beginning in the 1950's, when systematic aerial surveys were initiated by the Canadian Forest Service, and later by the Provincial government (FLNR 1996-2016). Dendroecological reconstructions of Douglas-fir tree-ring records can identify periods of sustained growth suppression (Alfaro et al. 1982; Swetnam and Lynch 1989; Swetnam and Lynch 1993; Campbell et al. 2006; Alfaro et al. 2014; Flower et al. 2014; Axelson et al. 2015; Ellis and Flower 2017), which provide evidence of past WSB defoliation. We integrated these two methods with forest ecosystem information to more fully describe the WSB outbreak history in southern interior forests and identify regional differences or similarities in outbreak timing and forest types affected. The purpose of this study was to elucidate a suite of unique parameters that more fully describe WSB Outbreak Regions in the interior Douglas-fir forests of B.C. by incorporating more precise information into work previously done by Maclauchlan et al. (2006). This previous study proposed five Outbreak Regions within the Thompson-Okanagan Forest Resource Region in the interior of B.C., based on the synchrony and amplitude of outbreaks documented since the early 1900's. Our three objectives were to more fully describe WSB Outbreak Regions by: (1) the analysis of the variability and distribution of ecosystems within historic documented outbreak areas; (2) identification of unique temporal and spatial patterns of WSB defoliation events by conducting a spatial overlay analysis of historic WSB defoliation (1909-2012); and, (3) the dendroecological reconstructions of growth suppression in Douglas-fir tree-rings caused by WSB defoliation (outbreak) events. This more robust description of WSB Outbreak Regions will facilitate targeted, long-term, preventative, and timely management of WSB-susceptible forests.

Methods

Describing ecosystem variability within WSB Outbreak Regions

The study area for this project was southern British Columbia (latitude 49-53^{o}N). Eleven of 15 unique WSB Outbreak Regions in the interior of B.C. were delineated and characterized by considering: outbreak history and host range; outbreak periodicity; forest attributes; ecosystem composition; natural topographic boundaries; and provincial resource district boundaries (Harris et al. 1985; Campbell et al. 2006; Maclauchlan et al. 2006; Maclauchlan and Brooks 2009; Alfaro et al. 2014; Axelson et al. 2015).

Two different but complementary regional ecosystem classification systems have been developed for B.C.: the Ecoregion Classification and Biogeoclimatic Ecosystem Classification (BEC) systems (Lloyd et al. 1990; Meidinger and Pojar 1991; Steen and Coupé 1997; Demarchi 2011; NTFSFMP 2013; FLNR 2014). The Ecoregion Classification describes regional-scale ecosystems based on the interaction of climate and physiography. The BEC system delineates ecological zones by vegetation, soils and climate, and is used most commonly in operational forest management. The WSB Outbreak Regions considers aspects of both systems but focuses primarily on the BEC system, as it is a more operationally applied system in B.C.

The majority of historical WSB defoliation in British Columbia has occurred in the IDF zone, although adjacent zones have also been affected (Maclauchlan et al. 2006). Using existing WSB Outbreak Region boundaries (Maclauchlan and Brooks 2009), natural topographic features, past defoliation events and the relative proportion of climatically-defined subzones in the IDF zone, new or more descriptive WSB Outbreak Regions were delineated. Within the IDF zone, subzones are delimited by temperature and precipitation regimes. Therefore, the proportion and distribution of IDF subzones were used as key factors in defining WSB Outbreak Region boundaries. The WSB Outbreak Regions sought to capture the biological and physical parameters that could influence WSB outbreak dynamics, such as major topographic impediments to dispersal, host range and connectivity, major water bodies that define geographic areas and regional climatic suitability. These geographic areas could in turn, facilitate specialized management strategies.

Spatial overlay analysis of historical WSB defoliation

Records of WSB defoliation date back to 1909 (Parfett et al. 1994; FLNR 1996-2016), but early records are sporadic, incomplete or have been transcribed to spatial files from written descriptions of defoliation events. Therefore, we used 1940 as the start-date and 2014 as the end-date to develop the 13 graphs depicting historic defoliation in WSB Outbreak Regions. A spatial overlay analysis coupled historic WSB defoliation (1909-2012) from B.C. Aerial Overview Survey data with BEC data. The analysis described and interpreted the duration, frequency and amplitude of WSB outbreaks across interior B.C. The ESRI ArcMap™ geoprocessing 'union' tool (available from Xtools Extension, Oregon State Department of Forestry) was used for the overlay analysis to remove overlapping defoliation polygons, while maintaining the attributes of each defoliation year. This allowed us to calculate the total number of years and the maximum number of years an area had been defoliated, and to report on non-cumulative area affected. Historical WSB defoliation records from aerial overview survey flights for B.C. were provided by the Canadian Forest Service, Pacific Forestry Centre (1909-1995) (Parfett et al. 1994) and the B.C. Ministry of Forests, Lands and Natural Resource Operations (1996-2015) (FLNR 1996-2016). Aerial overview data are collected annually by conducting fixed-wing surveys flown at 500 to 1,000 meters above ground level, and at speeds of 185 to 260 km/hr. The surveys identify and sketch map natural disturbances at scales of 1:100,000 to 1:250,000. Given the resolution of these surveys, they are viewed as coarse level surveys that can inform landscape level analysis and provide data that describe the gross area damaged, the location and severity of damage, and population trends. Polygons from hard copy maps are digitized, and pest damage and severity codes are assigned. Other attributes assigned per unique polygon include year of survey, forest resource district, and map reference (FLNR 1996-2016). From this database, it is possible to search or compile any combination of desired attributes.

Outbreak periods for the province of B.C. and each individual interior WSB Outbreak Region were identified, and the length of each period was calculated. The start was the year that defoliation was first mapped and the end was the last year of mapped defoliation. Potential outbreak periods were then checked spatially to determine if they were both spatially and temporally discrete. Checking and corroborating the results of the spatial overlay analyses allowed us to identify any small extensions of defoliation that crossed from one WSB Outbreak Region into an adjacent WSB Outbreak Region (usually areas less than 50 hectares, and of one-year duration). These were then considered part of the originating outbreak and the hectares were added to that outbreak. The spatial overlay analysis enabled us to determine how many total years any given area had been defoliated, how many consecutive years of defoliation had occurred in each defoliation event, and how much non-cumulative area had been affected over the course of an outbreak. Cumulative area defoliated was determined by merging all the years when WSB defoliation had occurred.

When determining outbreak periods for B.C., the total number of hectares affected can differ from the total of all WSB Outbreak Regions calculated separately. This is because more than one outbreak at a regional level can occur within a single provincial outbreak period. Therefore, an area could be defoliated and tallied more than once within the same provincial outbreak period.

The spatial overlay analyses were summarized and compared to the annual percentage of trees with growth suppression from a WSB event (as determined from tree-ring analysis, described below). To refine our comparison of detected defoliation and growth suppression, we intersected the WSB overlay analysis layer with the locations where tree cores were collected.

Dendrochronological reconstructions

Past WSB outbreaks were reconstructed using dendrochronology to compare the growth of host Douglas-fir trees against non-host pines, using a multi-step procedure as follows (Swetnam et al. 1985, Swetnam and Lynch 1989). In 2011-2012, we sampled 905 Douglas-fir host trees at 46 sites (average 20 cores per site) distributed across the 10 WSB Outbreak Regions that encompassed a range of defoliation histories in the southern interior of B.C. (Fig. 1). One increment core per tree was extracted from Douglas-fir trees that ranged in diameter from 8 to 67 cm at breast height (1.3 meters) and were growing in the dominant or sub-dominant canopy layers. Where possible, cores were collected from living canopy-dominant, non-host Ponderosa (n = 148) or lodgepole pine (n = 15) trees in close proximity to Douglas-fir sample sites. Following standard dendrochronological procedures (Stokes and Smiley 1968), cores were mounted on wooden supports and sanded with successively finer sandpaper to 400 or 600 grit. Each core was scanned to produce a high-resolution digital image (2,400 or 4,800 dpi). Ring-width series were measured using the program CooRecorder (Larsson 2011) and crossdated against trees of the same species using the program CDendro (Larsson 2011), which we verified using the program COFECHA (Holmes 1983).

To identify growth suppression events caused by WSB defoliation, long well-replicated chronologies for Douglas-fir and non-host trees growing under comparable environmental conditions must be used and the growth response of host and non-host species to climate must be similar. Ideally, these trees would be growing at the same sites (Swetnam et al. 1985, Swetnam and Lynch 1989); however, developing site-specific non-host chronologies was not possible in our study area. Few live, mature pines were available to sample, due to the recent mountain pine beetle outbreak that affected over 18.1 million hectares of pure and mixed-pine forests across interior B.C. (FLNR 2016). Following Axelson et al. (2015), we acquired existing non-host chronologies, including thirteen Ponderosa pine (Watson and Luckman 2001) and five lodgepole pine chronologies (Daniels and Watson 2003). Based on the location of non-host chronologies relative to each other and our study sites, we combined non-host chronologies with our newly sampled non-host trees to develop nine local and one regional Ponderosa pine chronologies, plus one regional lodgepole pine chronology. For each non-host chronology, we used the program COFECHA to verify crossdating and select the subset of highly-intercorrelated ring-width series to yield long, well-replicated non-host chronologies that extended to 2011.

Climate-growth analyses were conducted to test the assumption that Douglas-fir, Ponderosa pine and lodgepole pine respond to climate similarly and that the pines are suitable non-host controls for identifying past growth suppression events due to WSB defoliation (Swetnam et al. 1985). For Douglas-fir at each site, the subset of crossdated, highly-correlated ring-width series from canopy-dominant trees were used, since the growth of these trees was most likely to reflect the influences of regional climate (Fritts 1976). The regional lodgepole and Ponderosa pine chronologies and nine local Ponderosa pine chronologies were also assessed. For each chronology, individual ring-width series were detrended by fitting a negative exponential curve or straight line, then applying a 100-year spline with a 50% frequency response to the residuals using the program ARSTAN (Cook 1999). The resulting residual chronologies for each location and species were used in subsequent climate-growth analyses. Climate data were derived using ClimateWNA, a program that uses bilinear interpolation and elevation adjustments to downscale baseline gridded climate data to scale-free point data (Wang et al. 2012). Monthly total precipitation and monthly mean temperature records for 1901 to 2010 were derived for each Douglas-fir site. For the local and regional pine chronologies, climate data were derived for the sites from which the majority of cores were sampled. Using the program Dendroclim2002 (Biondi and Waikul 2004), correlation coefficients were calculated between each residual chronology and the monthly precipitation and temperature for a 16-month window from May of the year prior to ring formation through August of the year of ring formation. Bootstrapped confidence intervals were calculated to determine the significance of the correlation coefficients (Biondi and Waikul 2004).

The program OUTBREAK (Holmes and Swetnam 1996) was used to identify suppressions in host Douglas-fir trees that may have been caused by WSB defoliation. For these analyses, the crossdated ring-width series from all Douglas-fir trees, regardless of canopy position (dominant and subdominant), were detrended as described above for the climate-growth analyses (e.g., to account for biological age- and size-related trends and by fitting a 100-year 50% frequency response spline). To account for the effects of climatic variation on radial growth, the detrended ring-width indices for individual Douglas-fir trees at each site were corrected using the appropriate local or regional non-host pine standardized chronology. For sites in the four northern regions, analyses were repeated using the Ponderosa and lodgepole pine chronologies. User-defined criteria were applied to identify periods of suppression likely resulting from defoliation by WSB rather than other causes such as inter-annual climatic variation (Swetnam et al. 1985; Swetnam and Lynch 1989). After conducting a sensitivity analysis, growth suppressions in the corrected series for individual trees had to be ≥1.28 standard deviations below the mean and persistent for ≥8 years to be attributed to WSB defoliation. Similar thresholds have been applied to reconstruct WSB outbreaks in other studies conducted in British Columbia (Campbell et al. 2005, 2006; Alfaro et al. 2014; Axelson et al. 2015).

Historical outbreaks at each site were inferred for periods that included ≥5 Douglas-fir trees of which ≥50% exhibited growth suppressions meeting the criteria attributed to WSB defoliation. At the site level, we recorded the first year of growth suppression and the number of years that the trees remained suppressed to estimate the duration of each event. The estimated duration of growth suppression events (outbreaks) from tree-rings during the 20th century was compared to years of mapped defoliation using a two sample for means t-test and Pearson correlation. This comparison was done at three scales: (1) growth suppression of trees from all sites combined, compared to total annual defoliation mapped in B.C.; (2) growth suppression of trees from sites within each WSB Outbreak Region compared to annual defoliation within the WSB Outbreak Region; and, (3) growth suppression of trees within individual sites compared to years where annual defoliation was mapped in each site. We also summarized the number of years between WSB outbreak events, when no growth suppression was evident. We refer to this time interval as the "recovery period" because WSB populations are at low enough levels to no longer cause growth reduction in tree-rings.

Results

WSB Outbreak Regions –ecosystems and outbreaks

The first objective of this study was to analyse the variability and distribution of ecosystems within historic documented outbreak areas. Fifteen WSB Outbreak Regions are identified in B.C. (Table 1; Fig. 1). Ten WSB Outbreak Regions contain tree-ring chronology sites (Fig. 1), comprising interior Douglas-fir and are discussed in detail. Two WSB Outbreak Regions are located on the coast (Coast and Vancouver Island), and contain both coastal and interior Douglas-fir, while three Outbreak Regions are in the interior of B.C. (Okanagan NE, Quesnel Lake and Rocky Mountain-Kootenay Lake), contain susceptible interior Douglas-fir, and had incurred sporadic or no defoliation at the time of this study. The characteristics of 11 interior WSB Outbreak Regions are outlined in Appendix 1 describing the proportion of the WSB Outbreak Region land base located in the IDF, the geography, topography, and forest attributes.

WSB Outbreak Regions vary in size (Table 1) because of natural boundaries, location and connectivity of the primary host, Douglas-fir, ecosystem delineations (Fig. 2) and documented defoliation history. They are in part distinguished by the predominance and unique proportional blend of IDF subzones within these areas (Fig. 2). The majority of recorded WSB defoliation has occurred in the IDF zone (Table 2), particularly during the most recent and most dominant, Outbreak period 6 (1967-2012), which supports Maclauchlan et al. (2006). Each WSB Outbreak Region contains 2-6 IDF subzones (Fig. 2) with different proportional representation. Of the numerous IDF subzones, the IDFdk (dry, cool) dominates most interior WSB Outbreak Regions (Fig. 2) followed by the IDFxh (very dry, hot) and the IDFdm (dry, mild). From 1909-2012, the IDFdk and IDFxh sustained 1.3 million and 0.5 million hectares of defoliation, respectively in the province.

At a provincial scale, outbreak periods are defined by periods of documented defoliation followed by a year or more of no defoliation (Tables 2 and 3). There was time (1 to many years) between Outbreak periods 1-5 (1909-1950) (Table 3) when no defoliation was mapped in B.C. In contrast, defoliation was mapped continuously somewhere in the province during the most recent Outbreak period 6 (1967-2012) (Table 3). Despite there being no absolute cessation of defoliation within this 45-year period, we recognize three sub-outbreak periods across this massive geographic area.

Since defoliation records began in the early 1900s, each subsequent outbreak period has included increasingly more interior BEC zones, with Outbreak period 6 (1967-2012) being the most diverse in terms of the number and area (hectares) of ecosystems affected by WSB (Table 2). When the historic, cumulative aerial overview data were intersected with BEC zone, 67% of all WSB documented defoliation events occurred in the IDF and 33% within other ecosystems. Early defoliation events (1909-1930) were clearly in coastal BECs (Coastal Douglas-fir and Coastal Western Hemlock) (Table 2), with the first substantive defoliation documentation in the IDF (24,534 hectares) occurring in Outbreak period 4 (1943-50) and increasing exponentially in each successive outbreak within this BEC. This outbreak spanned the Coast and Lillooet WSB Outbreak Regions (Tables 2 and 3; Fig. 1), representing the transition from coastal to interior Douglas-fir, respectively. Outbreak period 1 (1909-1910) was documented entirely in the Vancouver Island WSB Outbreak Region in coastal Douglas-fir ecosystems. Defoliation in Outbreak period 2 (1916-1920) occurred in the IDFdc (dry, cold) and IDFww (wet, warm) within the Lillooet WSB Outbreak Region, which borders the Coast WSB Outbreak Region. Two spatially discrete defoliation events were recorded in Outbreak period 3 (1923-1930): one in the Vancouver Island WSB Outbreak Region affecting coastal BECs (coastal Douglas-fir); and one very small event (1,249 hectares) affecting IDF forests (dry, mild and very dry, hot subzones) in the Boundary WSB Outbreak Region. In Outbreak period 5 (1953-58) hectares defoliated in the

IDF continued to increase with just slightly less mapped (41% mapped in IDF forests) than in other ecosystems combined (Table 2; Fig. 3). Outbreak period 5 (1953-58) remained primarily in the Lillooet and Coast WSB Outbreak Regions (Tables 2 and 3) with some connecting drainages in the Kamloops WSB Outbreak Region also being affected. All regions except for the Vancouver Island WSB Outbreak Region experienced outbreaks events during Outbreak period 6 (1967-2012) (Table 3).

Documented WSB defoliation events were equally common in coastal and interior forests until the 1980s (Fig. 3). The first significant shift to interior, dry and transitional IDF forests in the 1980s through the 1990s occurred during Outbreak period 6 (1967-2012). Only in 1987 when the outbreak covered more than 833,000 hectares, was the defoliation equally distributed over IDF and non-IDF forests in B.C. In 1987, 423,876 hectares of defoliation were mapped in the Interior Cedar Hemlock BEC, largely in the Okanagan NE WSB Outbreak Region (Tables 2 and 3). This was a very eruptive expansion of WSB into these BECs, where both Douglas-fir and spruce were defoliated. From 2000 to 2012 in B.C., most outbreaks occurred in IDF forests (Fig. 3). Defoliation outside of the IDF typically occurred in adjoining BEC zones (either lower or higher in elevation).

Twelve BEC zones and 16 subzones were impacted in Outbreak period 6 (1967-2012), ranging from dry, low elevation sparsely treed sites to cold, higher elevation sites with mixtures of spruce. During this four-decade period, the first aerially recorded occurrence of defoliation in the Sub-boreal Pine Spruce (SBPS) and Sub-boreal Spruce (SBS) zones occurred, covering 36,830 hectares and representing about 1% of the total area defoliated (Table 2). Over 12% of documented defoliation occurred in moist, transitional interior Douglas-fir stands (Interior Cedar-Hemlock) where Douglas-fir grows in mixtures with other host and non-host species.

Many colder, higher elevation sites were affected, with almost 300,000 hectares defoliated in the Montane Spruce (MS) and Engelmann Spruce-Subalpine Fir (ESSF) combined, representing 9% of the total area affected in Outbreak period 6 (1967-2012). Some of the defoliation noted in the ESSF could be a function of mapping error associated with the coarse scale resolution of aerial surveys (e.g. the pen width on the aerial survey map represents 100M on the ground).

Temporal and spatial patterns of documented WSB defoliation events

The second objective of this study was to identify unique temporal and spatial patterns of WSB defoliation events by conducting a spatial overlay analysis of historic WSB defoliation. The spatial analysis was broken into three spatial scales: provincial, regional (WSB Outbreak Regions) and stand (tree core collection sites) level.

B.C.'s historic defoliation records show eight outbreaks: four outbreak periods from 1909 to 1950 (Table 3; Fig. 4) (Harris et al. 1985) and, four outbreak periods from 1953 to 2012. From 1909 to 1958 there were five recorded WSB outbreaks in B.C. lasting 2 to 8 years. 1967 to 2014 saw 48 continuous years of recorded defoliation in B.C. WSB defoliation events are clearly increasing in both amplitude (hectares affected) and duration since documentation of the defoliation began in the early 1900s.

The regional analysis of historic defoliation records shows shorter more eruptive patterns of defoliation across many of the southern (Lillooet, Boundary, Okanagan SE) and most northerly (Quesnel) WSB Outbreak Regions (Fig. 4), and some long, sustained outbreaks in the central regions from Kamloops through to Williams Lake in the Cariboo-Chilcotin (Axelson et al. 2015). Defoliation was recorded for 35 consecutive years in the Kamloops WSB Outbreak

Region, from 1976 through 2014, and could be considered one outbreak event. However, during this time there were at least two distinct surges, 1976-1994 and 2000-2014, with minimal defoliation recorded from 1995-1999. In the Kamloops WSB Outbreak Region, the average duration of defoliation events was 12.3 ± 11.3 (± S.E.) years. Comparatively, WSB defoliation built up in the Merritt WSB Outbreak Region during the mid-to-late 1990s then peaked through the 2000s. Very little defoliation was recorded in the region prior to this. The largest and most continuous areas of mapped defoliation occurred from 1999-2014 (16 years) and 2001-2014 (14 years) in the Williams Lake and 100 Mile House WSB Outbreak Regions respectively (Fig. 4). Unlike the defoliation patterns seen in Kamloops, these two regions saw continuous, sustained large areas of defoliation, with no distinct surges.

The Coast and Lillooet WSB Outbreak Regions defoliation events occurred at very regular intervals, lasting on average 8-10 years (Table 3; Fig. 4). The Quesnel Lake, Quesnel and Rocky Mountain - Kootenay Lake WSB Outbreak Regions had very short and spatially contained defoliation events, which generally lasted less than three years. The remaining eight WSB Outbreak Regions, in the central core of B.C.'s interior, had documented defoliation events ranging from five to nine years (Fig. 1; Table 3).

The most northerly WSB Outbreak Regions, Quesnel Lake and Quesnel, had only minor outbreak events, in 1987-88 and 2008-2012, respectively. The Williams Lake, Chilcotin and 100 Mile House WSB Outbreak Regions, which are located on the Cariboo-Chilcotin Plateau (Appendix 1), had few or no recorded defoliation events prior to the most recent outbreak in the late 1990s to early 2000s (Fig. 4). The largest documented defoliation in a single year was in the Okanagan NE WSB Outbreak Region in 1987 at 445,359 hectares. The defoliation increased three-fold from 1986 and then decreased by the same amount in 1988; a single eruptive event.

The second and third largest years of recorded defoliation both occurred in the Williams Lake WSB Outbreak Region in 2011 and 2006, at 305,715 hectares and 246,866 hectares, respectively (Fig. 4). Unlike the pattern seen in the Okanagan NE, defoliation was recorded in this Outbreak Region for 16 years over very large areas, ranging from 35,401-305,715 hectares before declining. Prior to the 2000s outbreaks erupting in these north-central Outbreak Regions, the largest recorded annual defoliation occurred in 1987, covering over 230,000 hectares in the Kamloops WSB Outbreak Region (Fig. 4). There was minimal recorded WSB defoliation in the Merritt WSB Outbreak Region until 1988 and then for 27 years (1988-2014) the area sustained observable levels of defoliation, peaking in the 2000s when recorded defoliation ranged from under 100 hectares to over 100,000 hectares (Fig. 4) with an average outbreak duration of 7.3 ± 5.9 years (± SE) (Table 3).

Prior to the 1980s, only the Coast and Lillooet WSB Outbreak Regions recorded annual defoliation near 100,000 hectares. The very steep, rugged Lillooet WSB Outbreak Region displayed six eruptive outbreak events with the most recent outbreak (2000-2013) (Fig. 4) being more prolonged than earlier events.

Dendrochronology – growth suppression events

We developed 46 new site-level ring-width chronologies for host Douglas-fir trees and 11 non-host chronologies, including one regional and nine local Ponderosa pine chronologies and one regional lodgepole pine chronology. The Douglas-fir chronologies ranged from 60 to 300 years, but most began in the late 1800s or early 1900s (Appendix 2). The non-host pine chronologies were 205 to 565 years, except one that was 114 years (Appendix 3). For chronologies of all three species, inter-series correlation values ranged from 0.621 to 0.843, indicating robust crossdating and a strong common signal among trees within stands. Mean sensitivity values ranged from 0.205 to 0.444, indicating moderate levels of year-to-year variation within the ring-width series.

Overall, Douglas-fir, Ponderosa pine and lodgepole pine residual ring-width chronologies responded to climate similarly, indicating both pine species could be appropriate climatic controls for the analysis and detection of past defoliation events of Douglas-fir (Appendix 4). Given the relatively warm, dry climate of our study area, ring widths were positively correlated with precipitation and negatively correlated with temperatures. The strongest and most consistent correlations were with growing season precipitation. Significant positive correlations were with precipitation in May to July of the year of ring formation (r = 0.19 to 0.44) and precipitation in August (r = 0.18 to 0.44) or September (r = 0.20 to 0.41) in the year prior to ring formation in northern or southern regions, respectively. Significant negative correlations with current May to July temperatures (r = 0.16 to 0.36) were weaker and less consistent among sites and species. Other significant correlations with either precipitation or temperature were sporadic among species, sites and months, with no consistent patterns. In the northern regions, correlations with current May to July precipitation were more similar between Douglas-fir (r = 0.19 to 0.32 for one to three consecutive months) and Ponderosa pine (0.24 to 0.30 for three consecutive months) than with lodgepole pine (r = 0.31 for May only). As well, the regional Ponderosa pine chronology was longer with higher inter-series correlation (r = 0.674) and mean sensitivity (MS = 0.286) values than the regional lodgepole pine chronology (r = 0.621 and MS = 0.224; Appendix 3). Combined, these outcomes suggest Ponderosa pine was a more suitable climatic control than lodgepole pine; all subsequent analyses for the northern regions were conducted using Ponderosa pine only.

We sought to detect and interpret periods of growth suppression events caused by WSB defoliation (suppression events) in Douglas-fir tree-rings at three scales: provincial (Fig. 5), WSB Outbreak Region (Fig. 6), and stand level (tree core collection sites) (Fig. 7). We detected at least one suppression event at all 46 study sites between 1716 and 2011. At the regional and stand scales, suppression events prior to 1925 were discrete, with growth suppression detected in only a few trees and stands between each event. After 1925, growth suppression events occurred at shorter intervals and were less synchronous; growth suppression events reconstructions were better replicated in recent decades than prior to 1925.

Provincial scale

At the provincial scale, the percent trees (all sites) showing growth suppression (Fig. 5) shows a sustained period of impact from the late-1980s until 2012, whereas total recorded WSB defoliation in B.C. (Figures 3 and 4), shows two distinct peaks of defoliation: in 1985-1992; and, again in 2001-2013. Provincially, eight growth suppression events were detected in southern B.C. from the mid-1700s to 2012 (>5 trees in analyses) (Fig. 5). We identified four growth suppression events during the 1800s (~1800s, 1850s, 1870s, and 1890s-1900s) supporting Alfaro et al. (2014) (Fig. 5), but only two growth suppression events in the 1900s (1930s-1960s and 1990s-2000s) and nothing in the 1970s as identified by Alfaro et al. (2014) and Campbell et al. (2006), highlighting how regionally variable WSB defoliation events can be. The growth suppressions recorded in the 1800s, 1850s, 1900s, 1950s and 1980s-2000s align with WSB tree-ring signatures in Oregon reported by Swetnam et al. (1995).

Regional scale

The occurrence and synchrony of growth suppression events were more variable at the regional scale. At the regional scale, 3-8 periods of growth suppression were identified in ten WSB Outbreak Regions (Table 4; Fig. 6). The average (± S.E.) duration of growth suppression events (10.0 ± 0.4 years) is longer (*t-test*, $P<0.05$) than the average outbreak duration calculated from defoliation records (7.6 ± 1.2 years) (Tables 3 and 6). Half the WSB Outbreak Regions with long enough chronologies showed growth suppression in the 1800s; 4 of 6 in the 1850s; and 5 of 7 in the 1880s showed growth suppression, supporting other reports for this time period (Campbell et al. 2006; Alfaro et al. 2014; Axelson et al. 2015). The growth suppression event of the late 1930s through 1940s-1950s was strong and relatively synchronized over all 10 WSB Outbreak Regions. Although a high proportion of trees showed growth suppression in all regions, the five north-central WSB Outbreak Regions (Quesnel, Chilcotin, Williams Lake, 100 Mile House, Kamloops) manifested the growth suppression event at a faster rate, earlier than the more southern WSB Outbreak Regions (Fig. 6). The very strong growth suppressions in the 1980s and then the 2000s were aligned with documented defoliation records but were less synchronized among regions than in previous outbreak events.

Periods of growth suppression in tree-ring chronologies ranged from 2 to 28 years (Table 4). The total length of growth suppression reflects the period of defoliation plus the recovery time for the trees. Within sites, the return interval (year 1 of one outbreak to year 1 of the next outbreak) between outbreaks ranged from 4 to 95 years with an average return interval for all sites of 39.5 ± 1.9 years, comparable to the 37 years documented by Alfaro et al. (2014) in the B.C. Okanagan.

Figure 6 illustrates how trees can experience many years of growth suppression from one year or many successive years of recorded defoliation events (e.g. Kamloops and Lillooet Outbreak Regions). The Lillooet WSB Outbreak Region has the longest record of documented defoliation and tree-ring growth suppression events (Fig. 6) and shows very regular growth suppression events going back over 300 years (Alfaro et al. 2014). The average duration of these events is 11.9 ± 1.5 years (±S.E.) with a return interval of 44.0 ± 5.1 years (±S.E.) (Table 4). Although the return interval is long, the recovery time is relatively small, averaging only 13.3 ± 0.3 years (±S.E.), when no trees are experiencing radial growth reductions from WSB defoliation. The Kamloops WSB Outbreak Region has strong periods of growth suppression back to the 1800s but lacks the 1850s growth suppression period that is dominant in the Lillooet WSB Outbreak Region (Fig. 6). There has been continuous documented defoliation in this region since 1976 with two distinct expansions in 1976-1993 and 2007-2011while 9-89% of trees show growth suppression over this 40 year period with no recovery period.

In the Merritt WSB Outbreak Region, the growth suppression event of the late 1980s-2000s coincides with recorded defoliation. The 1940s-1960s growth suppression event had no defoliation record for this time, but closely coincides with documented outbreaks to the south and west during that period (Harris et al. 1985). WSB populations may have been low within overstory trees and below the level of detection when conducting aerial surveys, but larvae may have caused higher levels of defoliation on the understory component of stands. This Outbreak Region also has a long outbreak history, but displays notable variations from the Lillooet WSB Outbreak Region. There is a moderate growth suppression event in Merritt during the 1830s that is not evident in Lillooet, and the large growth suppression event of the 1840s in Lillooet is absent from the Merritt tree-ring history. The average duration of growth suppression events in

Merritt is 10.4 ± 1.7 years (±S.E.) with a return interval of 46.7 ± 6.1 years (±S.E.) (Table 4). The recovery period is 9.5 ± 0.7 years (±S.E.).

Figure 6 also highlights how short defoliation events, or very low-level WSB populations (below the scale of detection in the aerial overview survey), may cause long periods of growth suppression. This was evident in the Boundary WSB Outbreak Region, where trees sampled showed growth suppression about three years prior to any mapped defoliation, and growth suppression was still prevalent in 28-80% of trees for nine years following the last mapped WSB defoliation.

Tree and stand scale

Growth suppression of trees at the stand level provide a much more defined periodicity of WSB growth suppression events compared to the provincial or regional scale. The occurrence of mapped WSB defoliation in tree core collection sites substantiates cause and effect (Fig. 7). WSB defoliation was present for one or more years in each period where trees showed periods of growth suppression (Fig. 7). However, it also clearly illustrates that in years with low levels of defoliation, which may not be discernible from the air, prolonged periods of growth suppression occurred on a proportionally high number of trees in a stand. Stand structure may lead aerial observers to underestimate actual defoliation; larger, overstory trees in a multi-layered stand may support many WSBs; however visible defoliation from the air may be minimal.

The Castle Rock tree core collection site (Quesnel WSB Outbreak Region) showed very pronounced, regular periods of growth suppression, as well as decades when trees displayed no growth suppression from WSB (Fig. 7). Although no defoliation was mapped prior to 2008, this site has experienced regular, episodic WSB defoliation events since the early 1900s, as evidenced by the high percentage of trees with growth suppression (Fig. 7). Defoliation was recorded in some locations in these more northern WSB Outbreak Regions during the 1990s. Growth suppression of trees in the Haines Lake site in the Chilcotin WSB Outbreak Region correlated with the last two major outbreak periods, with defoliation recorded in the site during both outbreaks. A small percentage of trees showed growth suppression four years prior to the aerial overview survey recording defoliation and continued after defoliation was no longer visible.

The Tom Cole tree core collection site located in the Lillooet WSB Outbreak Region shows clearly demarcated periods of growth reduction in the 1940s through mid-1960s, late 1970s through mid-1990s, and again in the 2000s. The 1960s and 1990s periods of growth suppression averaged 22.5 ± 2.5 years (± S.E.), and the current growth suppression period is ongoing (Fig. 7) although no defoliation has been recorded since 2010. Eight years of intermittent defoliation was mapped in both the 1990s and 2000s events, with 11 years between these two events when no defoliation was mapped.

The OK Falls and Rock Creek tree core collection sites are both located in the south, within the Okanagan SE and Boundary WSB Outbreak Regions, respectively (Fig. 1). The growth suppression pattern in both sites is eruptive, causing up to 100% of trees to suffer growth suppression (Fig. 7). There was only a very short time interval between the 1990s and 2000s suppression events where trees did not display growth suppression. However, the onset of growth suppression was rapid and complete once WSB populations were recorded at the OK Falls site. Prior to trees exhibiting growth suppression in the Rock Creek site, eight years of defoliation occurred in the site from 1979-1986. There was no recorded defoliation that coincided with the 2006-2011 growth suppression event, but this could be due to defoliation being below visual detection levels.

Discussion

At a landscape level, WSB populations are heterogeneously distributed and differ greatly in their density and consequently in their impact on host trees. WSB populations build episodically in many stands over large geographic areas and disperse to connected, suitable landscapes defoliating trees and stands for one to many years (Swetnam and Lynch 1993). Initiation, duration and periodicity of outbreaks are often synchronous across large landscapes (Campbell et al. 2005; Flower et al. 2014; Ellis and Flower 2017), yet vary at the tree and stand level (Swetnam and Lynch 1993; Swetnam et al. 1995; Ryerson et al. 2003; Campbell et al. 2006; Axelson et al. 2015), as seen in southern B.C. Defoliation records and growth suppression events in tree-rings each uniquely describe WSB outbreak dynamics and tree response at each spatial scale.

This study adds to the understanding of ecological habitats likely to experience WSB outbreaks, WSB outbreak periodicity and growth response of trees to WSB defoliation in southern B.C. (Campbell et al. 2006; Alfaro et al. 2014; Axelson et al. 2015). Provincially, six defoliation events were identified since the 1900s and eight distinct growth suppression events between 1716 and 2011. At the WSB Outbreak Region scale, up to seven growth suppression events were recorded in some regions where chronologies spanned over 300 years, with most showing two to three growth suppression events in the tree-ring chronologies over the past 100 years (Alfaro et al. 2014; Axelson et al. 2015). Growth suppression events at the regional scale are widespread and generally synchronous in key periods documented by others (Swetnam and Lynch 1993; Campbell et al. 2006; Alfaro et al. 2014; Axelson et al. 2015; Ellis and Flower 2017). However, the start year differs among regions. Some regions lack key suppression events and other regions have additional suppression events showing regional variability, particularly in the past half century (Ryerson et al. 2003; Axelson et al. 2015). WSB is likely synchronized over large areas via several potential mechanisms, including large-scale weather-related perturbations and dispersal of moths (Thomson et al. 1984; Kemp et al. 1985; Cooke et al. 2007). Southern B.C. is dominated by mountainous terrain and experiences more localized weather patterns, which may constrain moth dispersal. The Lillooet WSB Outbreak Region is very rugged and has a unique periodicity of recorded WSB outbreaks and growth suppression records. Further north in the Cariboo-Chilcotin plateau there is less topographic relief and climate, combined with stand composition and structure, is the main influence. The growth suppression periods in tree-ring records show WSB defoliation events have occurred for hundreds of years throughout the northern reaches of the Cariboo (Axelson et al. 2015) but the recent 2000s WSB outbreak appears to have been of higher severity (higher WSB populations) over a continuous geographic area than in the past. Defoliation was not recorded during the 1980s despite clear growth suppression in trees in four other, more northern WSB Outbreak Regions. The critical mass of WSB may have been feeding in the sub-dominant or understory layer where budflush is often earlier and more synchronized than in overstory trees (personal observations). The 2000s outbreak could have been a combination of mass moth dispersal from severe outbreaks to the south mixing with resident low level, established populations, coupled with more synchronized bud-insect phenology in all tree cohorts (Willhite and Stock 1983; Thomson and Benton 2007).

Thomson and Benton (2007) showed that warming winter temperatures on southern Vancouver Island promoted the earlier emergence of larvae while budflush remained constant, causing a desynchronization of insect and host. The documented defoliation data show an ecological shift from coastal or transitional ecosystems to Interior Douglas-fir ecosystems. This shift to interior and more northern IDF forests could highlight a more synchronized insect-host dynamic in these drier, colder ecosystems (Ryerson et al. 2003; Thomson and Benton 2007) in recent decades.

Axelson et al. (2015) identified 12 low intensity WSB outbreaks in the Cariboo, as far north as Williams Lake, over the past four centuries. Our data has identified outbreaks even further north, in the Quesnel and Chilcotin WSB Outbreak Regions, with a slightly shorter duration than the fifteen years noted by Axelson et al. (2015), and a return interval of thirty to over forty years.

Documenting WSB outbreaks in B.C. became more systematic, and coverage more complete starting in the 1950s (Harris et al. 1985; Westfall and Ebata 2007; Alfaro et al. 2014), but prior to this there were good records of the larger and more severe outbreaks throughout the province. The documented defoliation shows complementary but unique patterns to that of the tree-ring growth suppression. Defoliation was recorded for the first time in the Quesnel WSB Outbreak Region in 2003-2005, yet there was a 12-year growth suppression event that began in 1987 and affected most trees. WSB populations may have been below detection level in mature, overstory trees, but present at levels that could cause significant damage to sub-dominant trees in a stand. These sub-dominant or understory trees that were defoliated in past outbreaks are the trees from which cores were collected in this study that presently make up the dominant forest canopy. Many of the growth suppression events recorded in the more southern Outbreak Regions in the 1950s-1960s were probably in this sub-outbreak condition. In the 1940s, there was extensive selective harvesting that removed large overstory Douglas-fir and that coupled with the exclusion of fire that promoted multi-structured, often dense stands of WSB-susceptible forest (Swetnam and Lynch 1993; Ryerson et al. 2003; Maclauchlan and Brooks 2009; Flowers et al. 2014). Over the past 50-plus years, we have experienced changes in the climatic suitability of interior forest stands for WSB and potentially changes in the phenology of budflush, which is integral to the success of early instar WSB larvae. More recently, the death or removal of pine from many of these interior forests because of mountain pine beetle has further changed the micro-environment and canopy structure. This could be why the recent WSB defoliation events of the 2000s have been more severe and regionally larger events.

Defoliation records show that up to six discrete WSB growth suppression events occurred in the Lillooet WSB Outbreak Region over the past 100 years, compared to typically two or three outbreaks in the other regions. There were three prolonged growth suppression events over this 100-year period and no recovery period. This differs from the preceding 200 years, where recovery periods were frequent and of 20-plus year duration. The changed stand structure and increased density could in part be contributing to trees being more susceptible to WSB damage (Swetnam and Lynch 1993; Maclauchlan and Brooks 2009). The lag in response of tree-ring growth to defoliation is typically 1-to-3 years (Belyea 1952; Alfaro et al. 1982; Swetnam and Lynch 1989; Mason et al. 1997) and if recovery periods (no defoliation) are diminishing, then this may explain, why many trees in a stand are continually displaying growth suppression.

Comparison of defoliation to tree response in the form of growth suppression highlights the importance of detecting low-level WSB populations that may predispose trees to long periods of growth suppression when WSB populations increase in density and severity of feeding. Since the 1950s, the recovery period is becoming shorter in many WSB Outbreak Regions. This means that trees may be more susceptible to each successive defoliation event. Prompt detection of building WSB populations is even more critical as many of our low elevation Douglas-fir forests become more stressed with changing and unpredictable climate regimes (Swetnam and Lynch 1993; Volney and Fleming 2007; Ellis and Flower 2017).

The WSB Outbreak Region is a useful scale for forest managers to incorporate into land base planning. The delineation of WSB Outbreak Regions provides an ecologically based management unit at a moderate spatial scale, which describes outbreak periodicity, and can be used to inform forest management planning and treatments to help reduce future losses to WSB. The tree-ring chronologies provide site specific and regionally based tree response to WSB defoliation events and highlight the ever-shortening recovery period for trees affected by WSB.

This study identifies limitations and advantages in the two methods of detecting and interpreting WSB outbreaks: aerial mapping of defoliation and detecting growth suppression events through dendrochronology. Aerial surveys are limited in their ability to detect low (sub-outbreak) levels of defoliation. Stand, tree (Maclauchlan and Brooks 2009) and insect evaluations must be equal components in the interpretation of WSB outbreaks. We need more detailed data and linkages between WSB feeding on understory buds and radial tree-ring response. Projected changes in temperature and precipitation will likely affect the initiation and feeding patterns of future WSB outbreaks (Ellis and Flower 2017) and the susceptibility of interior Douglas-fir ecosystems. It is therefore important to elucidate how individual trees respond to low-level defoliation, or consecutive years of sub-outbreak WSB populations in ever changing climates.

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Appendix 1. Description of eleven WSB Outbreak Regions in British Columbia (Lloyd et al. 1990; FLNR. 2014)

Outbreak Region	% of Outbreak Region in IDF zone	Location[a]	Topography and stand features
Quesnel	1	Most northerly outbreak region. Bisected E-W by Fraser River IDFdk is on east edge of Chilcotin Plateau, near Soap Lake and Tingley Creek IDFxm is on both sides of Fraser River between south edge of Region and Moffatt.	Douglas-fir (Fd) on lower valley slopes and plateau. IDFdk – level to gentle slopes; Fd stands typically multi-aged and multi-storied with abundant, patchy Fd regeneration. IDFxm – moderate slopes; moderately closed canopy; single to multi-storied, depending on wildfire history.
Williams Lake	55	Bounded by Big Creek and Farwell Canyon on west edge; height of land between Williams Lake and Horsefly on east edge; Chimney Lake to Dog Creek to southeast, then south along Fraser River to Big Bar Creek	Very large, continuous areas of Fd. IDFdk – gently rolling, plateau sites IDFxm – lower valley slopes; patchy multi-storied stands
Chilcotin	16	Bisected N-S by Chilcotin River Bounded by Big Creek and Farwell Canyon on east edge Mostly Fd along Chilcotin River in Chilanko and Taseko River valleys on the Chilcotin Plateau, and in Homathko R. valley east of Coast Mountains.	IDFdk – level to gentle slopes; Fd stands multi-aged with abundant, usually patchy Fd regeneration; Pl stands typically even-aged with variable Fd understory
100 Mile House	65	Bounded by Fraser River to the west, the height of land in a N-S line through Bonaparte Plateau to the east, and Clinton to Loon Lake in the south	IDFdk – multi-aged, multi-storied Fd with patchy and abundant understory Fd; or Pl stands with Fd-dominated understory IDFxw – Fd with minor Ponderosa pine component; typically moderately open canopies with sparse clumps of Fd regeneration
Kamloops	50	Bisected by North Thompson River Bounded by Shuswap Highlands to the east and Hat Creek-Spences Bridge Valley to the west.	Diverse topography; large river systems. IDF on lower elevation slopes and plateau areas
Lillooet	28	Between Coast Mountains and Thompson-Okanagan Plateau	Rugged, steep, diverse topography with variable climate; many tree species. Fd spatially discrete due to steep topography
Okanagan NE	12	Includes Shuswap Lake and Adams Lake	Most Fd in west and central portion of Outbreak Region; dry Fd forests with multi-storied structure transition to moister Fd in single-canopy stands.
Okanagan SE	30	South Okanagan Valley, from Canada-USA border north to Enderby Bounded on east by Okanagan Highland and on west by height of land between Hedley and Pennask Lake	Variable, diverse topography centrally dominated by Okanagan Lake and surrounding dry valley. Fd spatially discrete, on low hills and drainages intersected by higher elevation stands and mountains.
Merritt	58	Cascade Mountains in west portion Thompson Plateau dominates east portion	Mountainous and steep in west; flat plateau in east.
Princeton	31	Similkameen Region, east of Cascade Mountains Includes Tulameen and Similkameen Rivers	Fd in valley bottoms, in narrow bands following major drainages.
Boundary	7	Includes Upper and Lower Arrow Lakes Bounded by Kettle River on west and Slocan River on east	Generally rolling; open stands

[a] BEC/IDF subzones: The first letter of each subzone describes relative precipitation (x=very dry; d=dry; m=moist; w=wet) and the second letter describes relative temperature (h=hot; w=warm; m=mild; k=cool; c=cold).

Appendix 2. List of 46 sites in southern British Columbia, grouped by Outbreak Region, where Douglas-fir (Fd), Ponderosa pine (Py) and lodgepole pine (Pl) cores were collected, noting: biogeoclimatic (BEC) subzone; latitude and longitude; elevation (metres above sea level); number of Douglas-fir and pine cores analysed; duration (start and end years), inter-series correlation and mean sensitivity of site-level Douglas-fir chronologies used to detect growth suppression events; density (trees per hectare) and percent mortality of Douglas-fir per plot; and number of years defoliated (total and consecutive) as recorded in the Aerial Overview Survey.

Outbreak		BEC	Latitude	Longitude	Elevation	No. cores		Duration	Inter-series	Mean	Trees	Percent	Defoliation (years)	
Region	Site	subzone[a]	(°N)	(°W)	(masl)	Fd	Pine	(years)	correlation	sensitivity	per ha	mortality	Total	Consec.
Quesnel	1[b]	IDFxm	52.502	122.501	790	20	15 Pl	1883-2011	0.779	0.266	172	0	3	2
Quesnel	2	IDFxm	52.521	122.409	710	20		1790-2011	0.782	0.362	198	0	3	2
Williams Lake	3	IDFdk	51.652	122.628	1,165	20		1711-2011	0.805	0.361	224	0	7	6
Williams Lake	4	IDFxm	51.797	122.586	1,010	21		1905-2011	0.818	0.444	169	23.7	5	3
Chilcotin	5	IDFxm	51.967	123.234	915	15		1808-2011	0.843	0.364	104	56.7	7	6
Chilcotin	6	IDFxm	51.974	123.219	820	15		1823-2011	0.787	0.405	69	58.0	7	6
Chilcotin	7	IDFxm	52.004	123.236	845	15		1917-2011	0.800	0.288	28	14.3	7	6
100 Mile	8[b]	IDFxw	51.115	121.572	1,090	20	18 Py	1685-2011	0.785	0.324	143	0	8	3
Lillooet	9	IDFxh	50.882	121.774	1,270	20		1899-2011	0.811	0.366	110	10.9	16	4
Lillooet	10	IDFxh	50.878	121.775	1,300	18		1895-2011	0.772	0.368	165	19.4	13	4
Lillooet	11	IDFdk	50.838	121.730	1,290	17		1879-2011	0.768	0.328	110	4.5	3	2
Lillooet	12	IDFdk	50.840	121.737	1,265	21		1899-2011	0.713	0.327	94	6.4	6	2
Lillooet	13	IDFxh	50.255	121.158	950	10		1698-2011	0.734	0.324	117	24.8	3	2
Lillooet	14	IDFxh	50.400	121.241	1,175	18		1733-2011	0.730	0.352	77	9.1	5	2
Lillooet	15	IDFxh	50.400	121.244	1,160	8		1744-2011	0.804	0.331	82	34.1	10	5
Kamloops	16	IDFdk	50.923	121.484	1,144	57		1807-2011	0.692	0.358	61	3.3	8	3
Kamloops	17	IDFxh	50.867	120.364	1,050	14		1858-2011	0.636	0.269	62	9.7	4	3
Kamloops	18	IDFxh	50.889	120.168	1,010	9		1881-2011	0.640	0.275	204	18.1	4	3
Kamloops	19	IDFxh	50.889	120.168	1,015	15		1951-2011	0.785	0.271	70	51.0	3	3
Kamloops	20	PPxh	50.888	120.190	701	12		1904-2011	0.803	0.267	88	21.6	4	3
Kamloops	21	IDFxh	50.892	120.334	970	15		1759-2011	0.671	0.328	116	16.4	5	3
Kamloops	22	IDFxh	50.987	120.203	800	15		1833-2011	0.666	0.292	223	0	5	4
Kamloops	23	IDFxh	50.991	120.205	825	16		1869-2011	0.699	0.257	166	29.5	5	3
Kamloops	24	IDFxh	50.744	120.119	835	20		1917-2011	0.764	0.330	183	11.5	6	3

Kamloops	25	IDFdk	50.905	120.712	1,080	20		1814-2011	0.715	0.302	71	22.5	5	3
Kamloops	26	IDFxh	51.652	122.628	1,220	15		1822-2011	0.709	0.322	88	15.9	2	1
Kamloops	27[b]	IDFdk	50.674	120.663	1,095	39	17 Py	1799-2011	0.736	0.345	133	23.0	9	4
Kamloops	28	IDFxh	50.473	119.801	710	10		1901-2011	0.651	0.251	175	35.4	2	1
Kamloops	29	IDFxh	50.344	119.952	720	14		1907-2011	0.630	0.273	45	8.9		
Kamloops	30	IDFdk	50.528	119.882	970	14		1934-2011	0.583	0.205	127	30.7	3	1
Kamloops	31	IDFdk	50.521	119.876	1,060	14		1905-2011	0.706	0.268	66	22.7	3	3
Kamloops	32	IDFdk	50.528	119.882	1,090	17		1781-2011	0.758	0.250	121	4.1	9	3
Kamloops	33	IDFdk	50.586	119.853	967	45		1891-2011	0.658	0.278	42	16.7	5	2
Merritt	34	IDFdk	49.953	120.898	1,176	44		1873-2011	0.621	0.262	104	8.7	7	3
Merritt	35[b]	IDFxh	50.012	120.969	1,106	39	10 Py	1917-2011	0.731	0.320	108	0	7	3
Merritt	36[b]	IDFdk	50.162	120.750	1,155	16	5 Py	1893-2012	0.779	0.300	193	31.0	10	5
Merritt	37	IDFdk	50.304	120.800	1,255	20		1724-2012	0.768	0.349	161	1.0	5	3
Merritt	38[b]	IDFxh	50.193	120.625	1,040	29	5 Py	1930-2012	0.707	0.276	81	13.6	5	3
Princeton	39[b]	IDFdk	49.477	120.605	1,200	18	8 Py	1908-2011	0.635	0.225	166	4.2	5	2
Princeton	40[b]	IDFxh	49.529	120.565	1,130	15	34 Py	1937-2011	0.720	0.340	78	16.7	7	5
Okanagan SE	41	IDFdk	49.453	119.813	1,520	13		1880-2011	0.604	0.207	94	4.3		
Okanagan SE	42[b]	IDFxh	49.338	119.458	1,130	20	4 Py	1890-2011	0.655	0.281	136	14.0	9	6
Okanagan SE	43	IDFdk	49.262	119.723	1,305	17		1720-2011	0.692	0.284	84	6.0	8	3
Okanagan SE	44[b]	IDFxh	49.790	119.779	990	28	4 Py	1925-2011	0.649	0.341	47	31.9	13	6
Boundary	45	IDFxh	49.037	119.042	830	15		1914-2011	0.724	0.269	180	6.7	11	6
Boundary	46[b]	IDFxh	49.037	119.042	880	5	15 Py	1879-2011	0.655	0.314	145	3.4	7	3

[a] IDF refers to the Interior Douglas-fir biogeoclimatic zone. The first letter of each subzone describes relative precipitation (x=very dry; d=dry; m=moist; w=wet) and the second letter describes relative temperature (h=hot; w=warm; m=mild; k=cool; c=cold).

[b] Non-host pine trees were sampled in stands surrounding this site.

Appendix 3. Crossdated ring-width chronologies of non-host lodgepole pine and ponderosa pine growing in 10 WSB Outbreak Regions of B.C. The number of cores per chronology was a combination of newly collected cores and existing chronologies (Daniels and Watson (2003) for lodgepole pine; Watson and Luckman (2001) for ponderosa pine).

Non-host species and WSB Outbreak Region	Plots	No. cores	Duration (years)	Inter-series correlation	Mean sensitivity
Lodgepole pine					
Quesnel, Williams Lake, Chilcotin, 100 Mile	1–8	118	1775-2011	0.621	0.224
Ponderosa pine					
Quesnel, Williams Lake, Chilcotin, 100 Mile, Lillooet	1–12	50	1633-2011	0.674	0.286
Lillooet	13–15	61	1468-2011	0.649	0.356
Kamloops	16–27	62	1523-2011	0.728	0.362
Kamloops	28–33	21	1571-2011	0.640	0.276
Merritt	34–35	44	1448-2011	0.666	0.333
Merritt	36–38	46	1448-2012	0.666	0.333
Princeton	39–40	35	1897-2011	0.661	0.309
Okanagan SE	41–43	19	1806-2011	0.711	0.298
Okanagan SE	44	46	1589-2011	0.625	0.300
Boundary	45–46	60	1584-2011	0.647	0.287

Appendix 4. Significant correlation function coefficients ($p < 0.05$) between residual ring-width chronologies and climate variables for the 16 months from May prior to the year of ring formation (May to December in italics) though August of the year of ring formation (December to August in regular font). Sites are arranged by Region. Each site-level chronology of host Douglas-fir (Fd) was compared with regional or local non-host lodgepole (Pl) or ponderosa (Py) pine chronologies in the shaded panels below them.

Region	Species	Site	Precipitation																Temperature															
			M	*J*	*J*	*A*	*S*	*O*	*N*	*D*	J	F	M	A	M	J	J	A	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	J	F	M	A	M	J	J	A
Quesnel	Fd	1			*0.21*	*0.24*									0.25	0.32															-0.21	-0.27		
	Fd	2													0.26	0.26																-0.24		
Williams Lake	Fd	3				*0.33*			*0.23*						0.25	0.27											0.17			0.16				
	Fd	4				*0.24*			*0.22*	*0.21*						0.31											0.19					-0.18		
Chilcotin	Fd	5				*0.29*									0.21	0.27	0.22																-0.2	
	Fd	6				*0.35*									0.19	0.22	0.22														-0.22		-0.20	
	Fd	7				*0.33*			*0.23*	*0.31*						0.32	0.26								*0.20*						-0.20	-0.24	-0.3	
100 Mile	Fd	8		*0.19*	*0.25*	*0.32*								0.20	0.19						*-0.21*				*0.18*	*0.19*								
Lillooet	Fd	9				*0.29*				*0.30*					0.19	0.31		-0.2																
	Fd	10				*0.23*				*0.27*					0.20	0.24																		
	Fd	11				*0.27*	*0.20*		*0.16*	*0.16*																								
	Fd	12				*0.24*										0.26											0.17							
	Pl		*0.22*			*0.44*	*0.21*								0.31												0.25			0.26				
	Py		*0.19*			*0.42*	*0.29*								0.24	0.30	0.29									*0.26*	0.24			0.32				
Lillooet	Fd	13		*0.22*											0.24										*0.22*		0.28							
	Fd	14													0.19																			
	Fd	15												0.18								*0.22*		*0.17*		*0.20*								
	Py					*0.18*		*0.22*							0.22	0.36																		
Kamloops	Fd	16				*0.28*									0.25	0.37										*0.18*								
	Fd	17				*0.40*									0.19	0.30					*0.26*											-0.20		
	Fd	18								*0.23*					0.31	0.30	0.23							*0.18*								-0.24	-0.3	
	Fd	19							*0.32*	*0.29*	0.25					0.36																		
	Fd	20				*0.26*									0.24	0.28	0.24															-0.21	-0.2	
	Fd	21				*0.24*									0.24	0.33																-0.27	-0.20	
	Fd	22				*0.29*									0.35	0.25			*0.19*													-0.21		
	Fd	23				*0.44*									0.24	0.30			*0.22*	*0.23*														
	Fd	24									0.22				0.28	0.31								*0.18*								-0.22		
	Fd	25			*0.22*	*0.26*	*0.24*								0.30	0.39																-0.27	-0.3	
	Fd	26				*0.29*	*0.20*								0.36	0.29	0.23											0.20						
	Fd	27				*0.20*									0.36	0.35	0.18															-0.31	-0.2	
	Py					*0.30*	*0.25*	*0.21*							0.31				*0.25*	*0.22*												-0.20		
Kamloops	Fd	28					*0.21*		*0.26*						0.36					*0.22*														
	Fd	29					*0.30*	*0.24*							0.29					*0.22*				*0.20*										
	Fd	30													0.34			0.25		*0.24*														
	Fd	31					*0.21*								0.31	0.28								*0.27*								-0.21		
	Fd	32				*0.33*																*-0.18*												-0.2
	Fd	33				*0.19*	*0.26*								0.30	0.26								*0.28*							-0.21			
	Py					*0.19*	*0.32*		*0.22*						0.29								*-0.20*											
Merritt	Fd	34				*0.27*	*0.25*								0.28	0.27	0.29															-0.21		
	Fd	35					*0.24*		*0.16*						0.34	0.24	0.22							*0.27*										
	Py						*0.24*					0.24				0.23	0.36					*0.17*										-0.19		
Merritt	Fd	36					*0.21*								0.31	0.24	0.34						*-0.18*	*0.19*										
	Fd	37				*0.29*	*0.21*									0.23	0.28																	
	Fd	38													0.44					*0.23*				*0.29*								-0.36	-0.2	
	Py		*0.19*			*0.20*	*0.22*					0.25			0.21	0.25	0.37															-0.25		
Princeton	Fd	39				*0.18*									0.25	0.22															-0.20			
	Fd	40					*0.21*	*0.29*				0.25		0.22	0.38	0.28																		
	Py						*0.17*		*0.23*						0.25	0.25	0.27												-0.20					
Okanagan SE	Fd	41			*0.25*	*0.22*	*0.29*							0.24	0.34	0.29	0.23		*0.19*															
	Fd	42																														-0.19		
	Fd	43					*0.31*							0.21	0.35	0.38																		
	Py					*0.18*	*0.38*								0.40	0.40	0.39																-0.2	
Okanagan SE	Fd	44					*0.29*								0.29	0.27										*0.19*								
	Py					*0.20*	*0.41*		*0.23*						0.24	0.24	0.37						*0.17*				0.19						-0.3	
Boundary	Fd	45					*0.26*				0.24			0.31	0.35	0.29										*0.28*								
	Fd	46		*0.24*								0.30		0.26	0.35																			
	Py					*0.22*	*0.40*								0.41	0.34	0.34					*-0.19*					0.25							

Table 1. List of 15 WSB Outbreak Regions showing the total area (hectares) of each region, the area of each region defoliated (as recorded in Aerial Overview Survey data, 1909-2014) and the percent of each region defoliated by WSB over this period.

WSB Outbreak Region	Hectares		Percent of Outbreak Region defoliated 1909-2014
	Area of Outbreak Region	Area defoliated 1909-2014	
Quesnel Lake	735,454	11,035	1.5
Quesnel	2,077,233	20,714	1.0
Williams Lake	1,122,445	457,686	40.8
Chilcotin	2,248,303	112,988	5.0
100 Mile House	953,648	440,092	46.1
Kamloops	1,060,364	481,149	45.4
Lillooet	1,157,531	339,012	29.3
Okanagan NE	3,499,506	612,009	17.5
Okanagan SE	1,132,720	253,366	22.4
Merritt	632,747	230,307	36.4
Princeton	513,833	114,965	22.4
Boundary	2,048,074	70,530	3.4
Rocky Mtn -Kootenay Lake	4,107,146	13,756	0.3
Coast	6,394,823	327,790	5.1
Vancouver Island	2,104,321	34,201	1.6
Total	27,683,828	3,485,399	

Table 2. Hectares (ha) defoliated by BEC zone in the 6 modern outbreak periods in B.C., as defined by defoliation records, with 6 being the most recent outbreak event. Time span of each outbreak is shown below outbreak number.

		Modern outbreak periods (ha defoliated)						
BEC	BEC	1	2	3	4	5	6	
Code	Description	(1909-10)	(1916-20)	(1923-30)	(1943-50)	(1953-58)	(1967-2012)	Total Ha
BG	Bunchgrass					2,060	24,301	26,362
PP	Ponderosa Pine				1,559	7,414	63,184	72,157
IDF	Interior Douglas-fir		87	1,057	24,534	88,510	2,352,565	2,466,752
ICH	Interior Cedar-Hemlock						423,876	423,876
MS	Montane Spruce			193		2,639	192,245	195,077
ESSF	Engelmann Spruce-Subalpine Fir				148	5,480	105,735	111,364
CWH	Coastal Western Hemlock	1,726		2,312	10,129	98,098	165,554	277,819
CDF	Coastal Douglas-fir	16,757		26,069				42,826
CMA	Coastal Mountain-heather Alpine				9	957	4,294	5,260
IMA	Interior Mountain-heather Alpine					268	2,017	2,285
MH	Mountain Hemlock				159	2,482	21,705	24,347
SBPS	Sub-Boreal Pine-Spruce						6,176	6,176
SBS	Sub-Boreal Spruce						30,654	30,654
Total		18,483	87	29,631	36,538	207,909	3,392,307	3,684,954

Table 3. Summary of WSB defoliation events as recorded by the Aerial Overview Surveys in British Columbia and 15 WSB Outbreak Regions, listing the number of modern outbreak periods, average duration of outbreaks (years ± S.E.); hectares defoliated in each outbreak (non-cumulative); and total hectares defoliated. Outbreaks periods are listed from earliest recorded (1) to most recent (outbreak 6 being the most recent or current outbreak).

Outbreak Region	No. of outbreaks	Outbreak duration[a] (avg. ± S.E.)	Outbreak period (hectares defoliated) 1 (1909-10)	2 (1916-20)	3 (1923-30)	4[b] (1943-50)		5 (1953-58)	6[c] (1967-2012)			Total hectares
British Columbia	6	12.5 ± 6.8	18,482	85	29,631		36,538	207,908			3,392,306	3,684,950
Quesnel Lake	1	1.0							967			967
Quesnel	3	2.7 ± 1.2							411	20,429		20,842
Williams Lake	2	8.0 ± 7.0							932	454,682		455,549
Chilcotin	2	5.0 ± 4.0							112,941			112,984
100 Mile House	3	8.7 ± 2.8							35,609	11,775	435,647	483,033
Kamloops	3	12.3 ± 11.3				18		7,704	472,906			480,628
Lillooet	6	10.2 ± 4.2		85		14,930	5,831	49,072	266,264	186,102		522,285
Okanagan NE	4	5.8 ± 2.1							44,353	565,190	90,148	699,704
Okanagan SE	2	12.5 ± 1.5							188,517	177,317		365,539
Merritt	4	7.3 ± 5.9							3,288	1,021	227,617	231,854
Princeton	3	6.0 ± 3.2							797	262	114,598	115,658
Boundary	3	7.7 ± 3.8			1,249				21,963	62,749		85,962
Rocky Mtn-Kootenay Lk	1	1.0							13,666			13,667
Coast	5	8.4 ± 2.0				19,310		151,132	198,979	30,177	85,306	484,907
Vancouver Island	2	3.0 ± 1.0	18,482		31,363							49,846

[a] The average (±S.E.) outbreak duration across all outbreak regions is 7.6 ± 1.2 years.
[b] Outbreak 4 is comprised of 1-2 eruptive defoliation cycles dependent upon Outbreak Region
[c] Outbreak 6 is comprised of 1-3 eruptive defoliation cycles dependent upon Outbreak Region

Table 4. Length and number of WSB outbreaks in tree-ring chronologies, number of plots, and average outbreak duration, return interval and recovery period. The number of outbreaks are determined from the number of prolonged periods of growth suppression in trees (suppression events with >5 trees in analysis).

	Outbreak chronology			Average (years) ± SE		
Outbreak Region	Length (years)	No. Outbreaks	No. Plots	Duration	Return Interval	Recovery period [a]
Quesnel	129-222	6	2	9.6 ± 1.8	33.4 ± 5.9	12.5 ± 0.03
Williams Lake	107-301	3	2	8.2 ± 0.8	43.0 ± 11.1	12.2 ± 1.2
Chilcotin	95-204	4	3	13.5 ± 2.3	45.9 ± 7.1	15.0 ± 1.2
100 Mile House	327	6	1	9.2 ± 2.0	38.5 ± 5.4	9.3
Kamloops	61-279	5	18	9.3 ± 0.6	39.2 ± 3.5	6.8 ± 0.5
Lillooet	113-314	7	5	11.9 ± 1.5	44.0 ± 5.1	13.3 ± 0.3
Okanagan SE	87-292	6	4	9.5 ± 1.8	32.4 ± 9.5	11.2 ± 0.9
Merritt	83-289	7	5	10.4 ± 1.7	46.7 ± 6.1	9.5 ± 0.7
Princeton	75-104	3	2	10.5 ± 4.4	32.0 ± 17.0	5.0 ± 1.6
Boundary	98-133	3	2	9.0 ± 1.2	33.3 ± 6.7	12.8 ± 0.8
Total / Average	160	5	46	10.0 ± 0.4	39.5 ± 1.9	9.5 ± 0.6

[a] The number of years when trees do not show growth suppression from a WSB event.

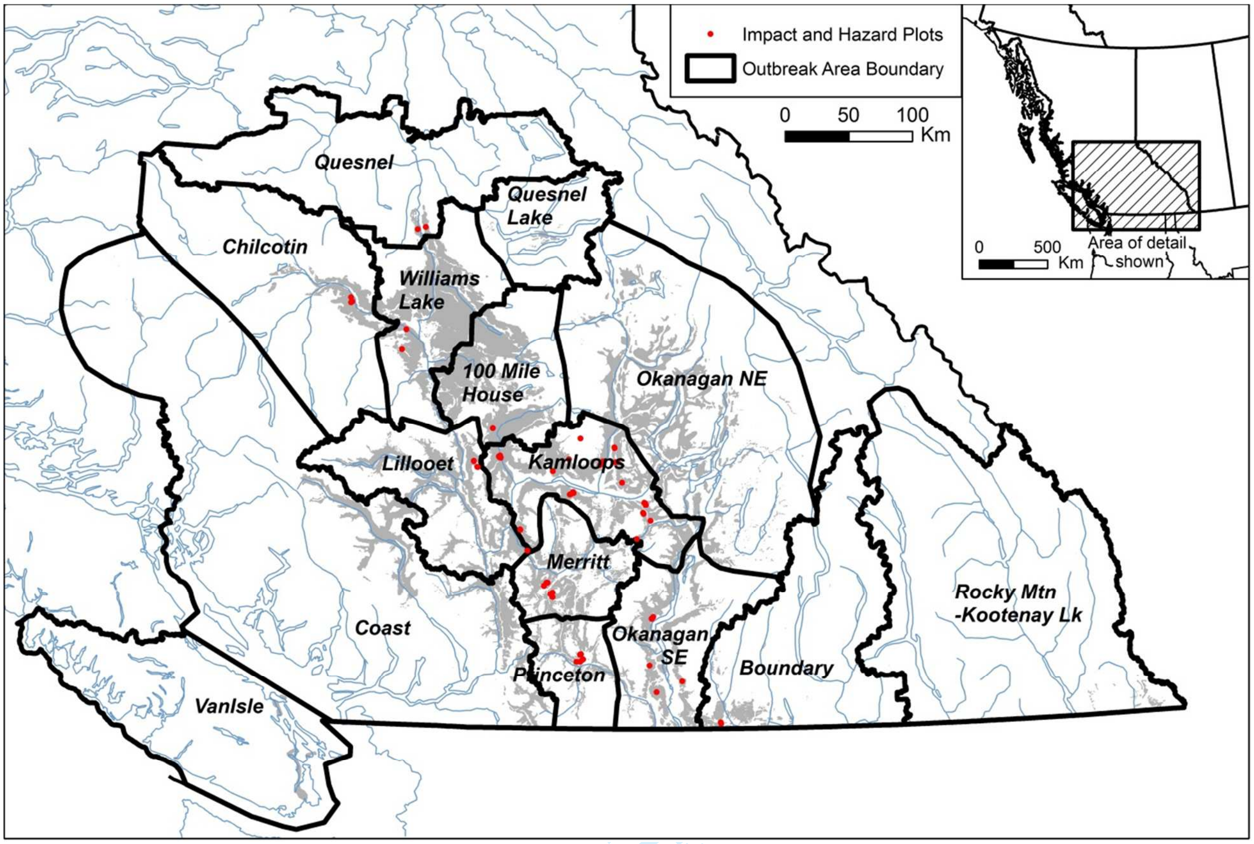
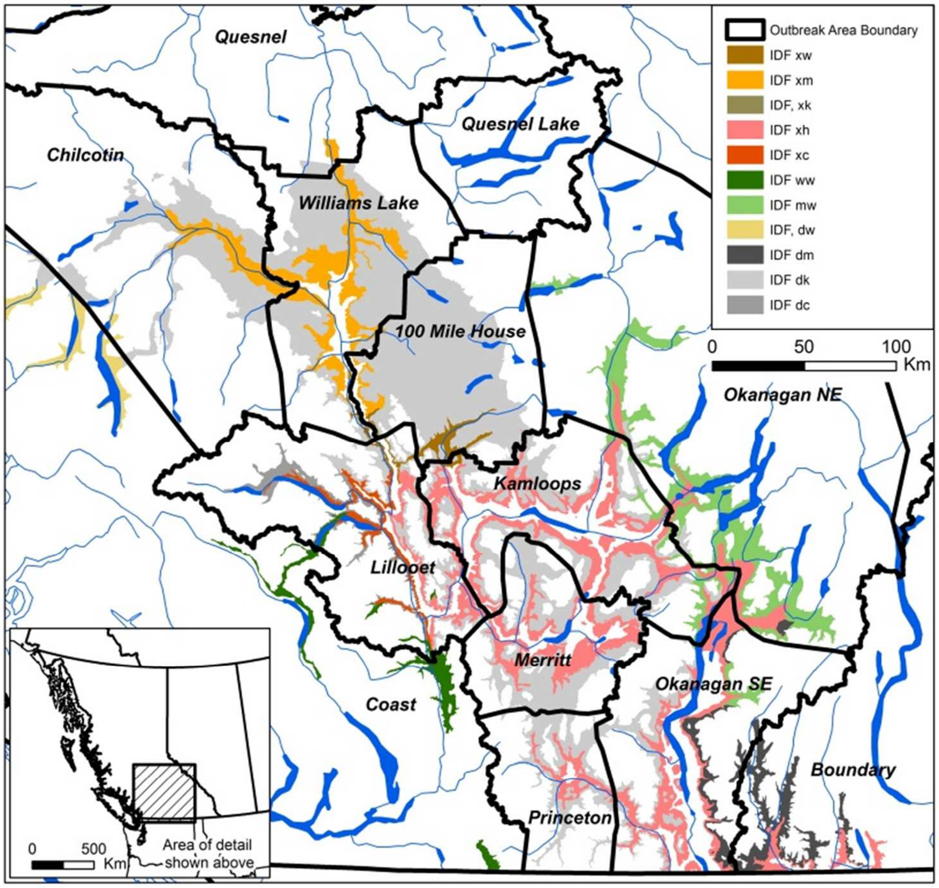
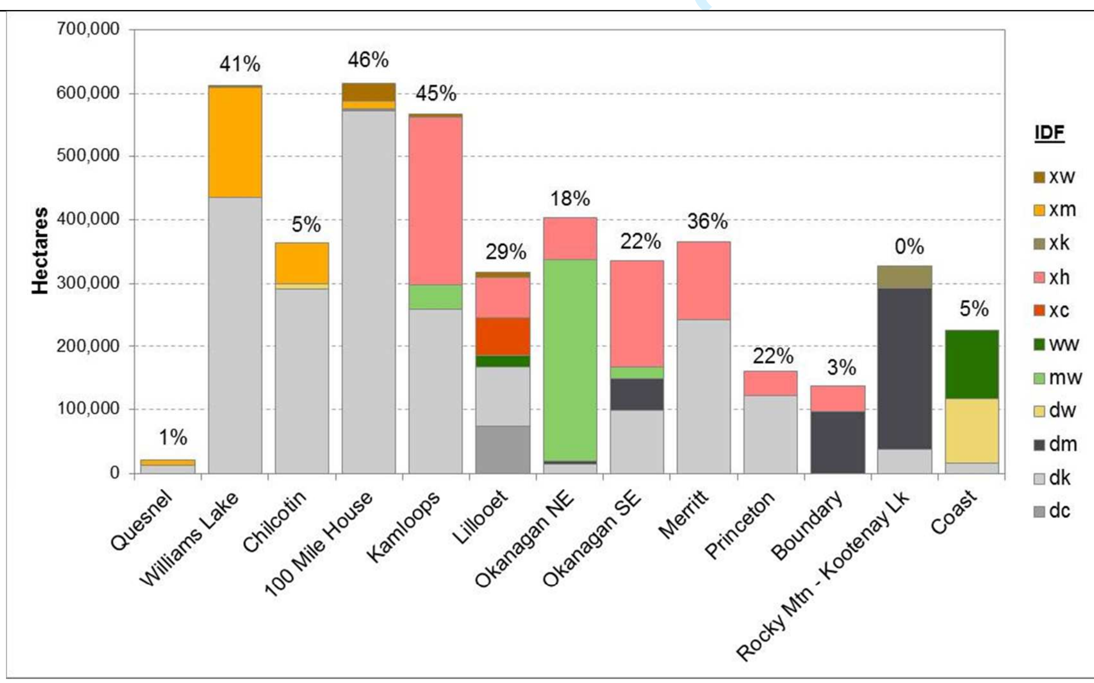


Figure 1. Boundaries of 15 WSB Outbreak Regions in B.C. (heavy black lines) and 46 tree-ring chronology sites (red dots), and area of historic defoliation in grey (1909-2014).


Outbreak Area Boundary
IDF xw
IDF xm
IDF, xk
IDF xh
IDF xc
IDF ww
IDF mw
IDF, dw
IDF dm
IDF dk
IDF dc
0 50 100 Km
Quesnel
Quesnel Lake
Chilcotin
Williams Lake
100 Mile House
Okanagan NE
Kamloops
Lillooet
Merritt
Okanagan SE
Coast
Boundary
Princeton
0 500 Km
Area of detail shown above

a)


700,000
600,000
500,000
400,000
300,000
200,000
100,000
0
Hectares
1%
41%
5%
46%
45%
29%
18%
22%
36%
22%
3%
0%
5%
Quesnel
Williams Lake
Chilcotin
100 Mile House
Kamloops
Lillooet
Okanagan NE
Okanagan SE
Merritt
Princeton
Boundary
Rocky Mtn - Kootenay Lk
Coast
IDF
xw
xm
xk
xh
xc
ww
mw
dw
dm
dk
dc

b)

Figure 2. Distribution of Interior Douglas-fir (IDF) subzones within 13 WSB Outbreak Regions. a) Map of IDF subzones in WSB Outbreak Regions. b) Graph of the area defoliated (cumulative hectares) in each IDF subzone by WSB Outbreak Region. The percent of each WSB Outbreak Region defoliated (1909-2014) is shown above each bar. The first letter of each subzone describes relative precipitation (x=very dry; d=dry; m=moist; w=wet) and the second letter describes relative temperature (h=hot; w=warm; m=mild; k=cool; c=cold). Additional information about subzones can be found in Appendix 1.

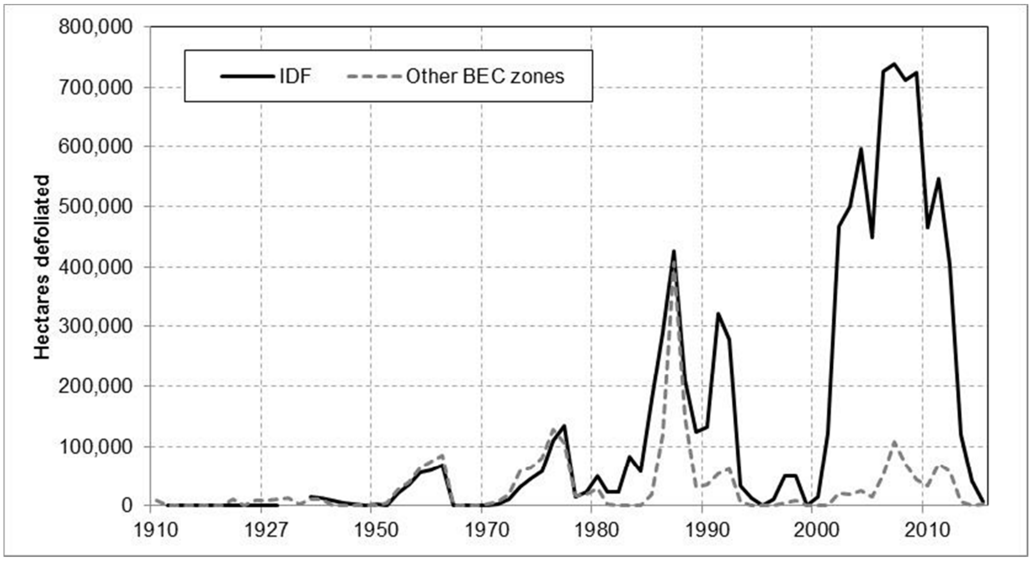


Figure 3. Hectares defoliated by WSB in British Columbia as recorded in the annual Aerial Overview Surveys (CFS 1909-1995; FLNR 1996-2014) comparing hectares defoliated in the Interior Douglas-fir (IDF) biogeoclimatic zone to hectares defoliated in all other biogeoclimatic zones combined.

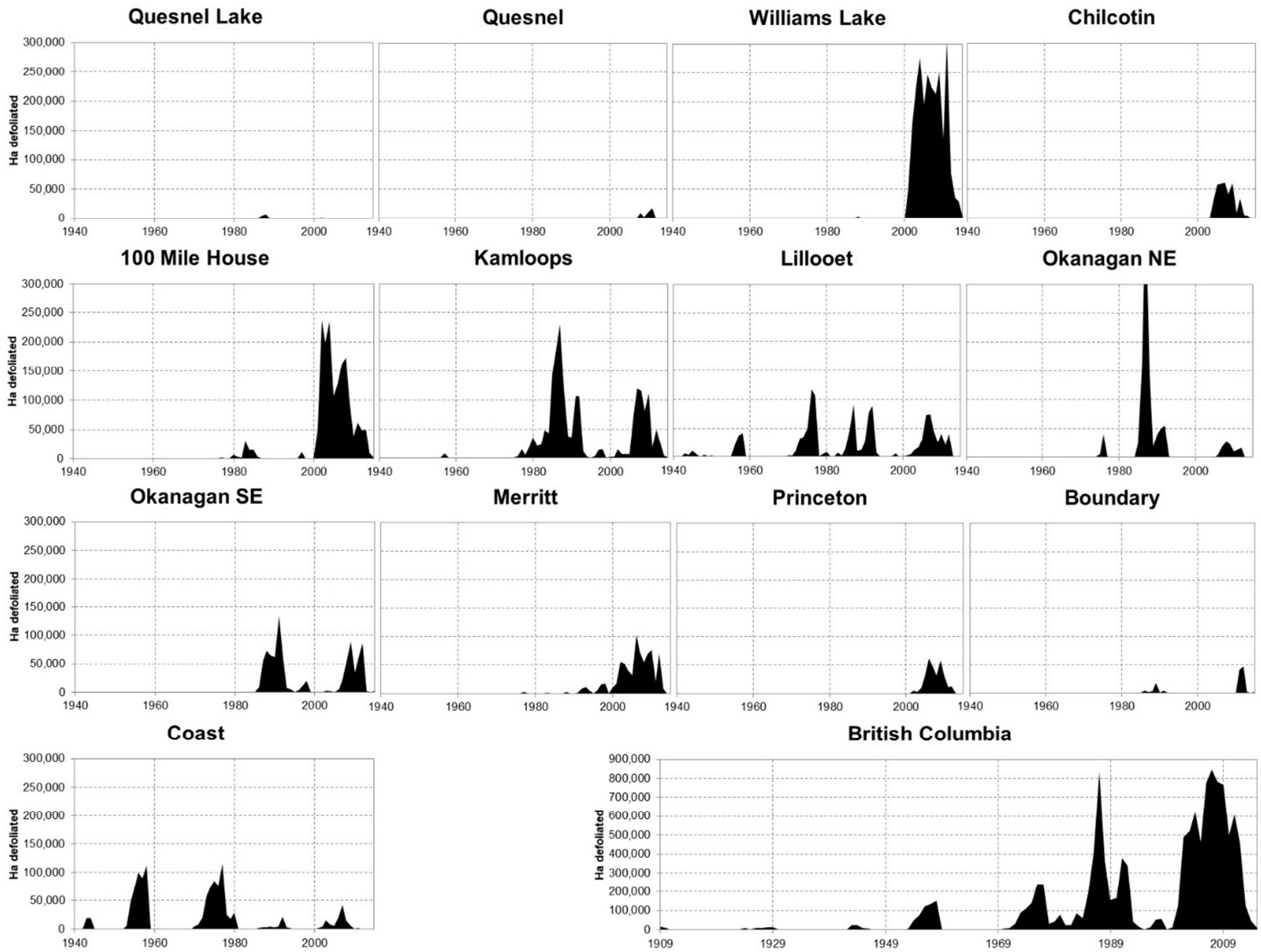


Figure 4. Hectares defoliated in 13 WSB Outbreak Regions (1940-2014) and British Columbia (1909-2014) as recorded in the B.C. Aerial Overview Surveys database (CFS 1909-1995; FLNR 1996-2014). The Vancouver Island Outbreak Region has had no recorded defoliation since 1930 and the Rocky Mountain-Kootenay Lake Outbreak Region recorded defoliation for the first time in 2014. These two regions are not included in the above graphs.

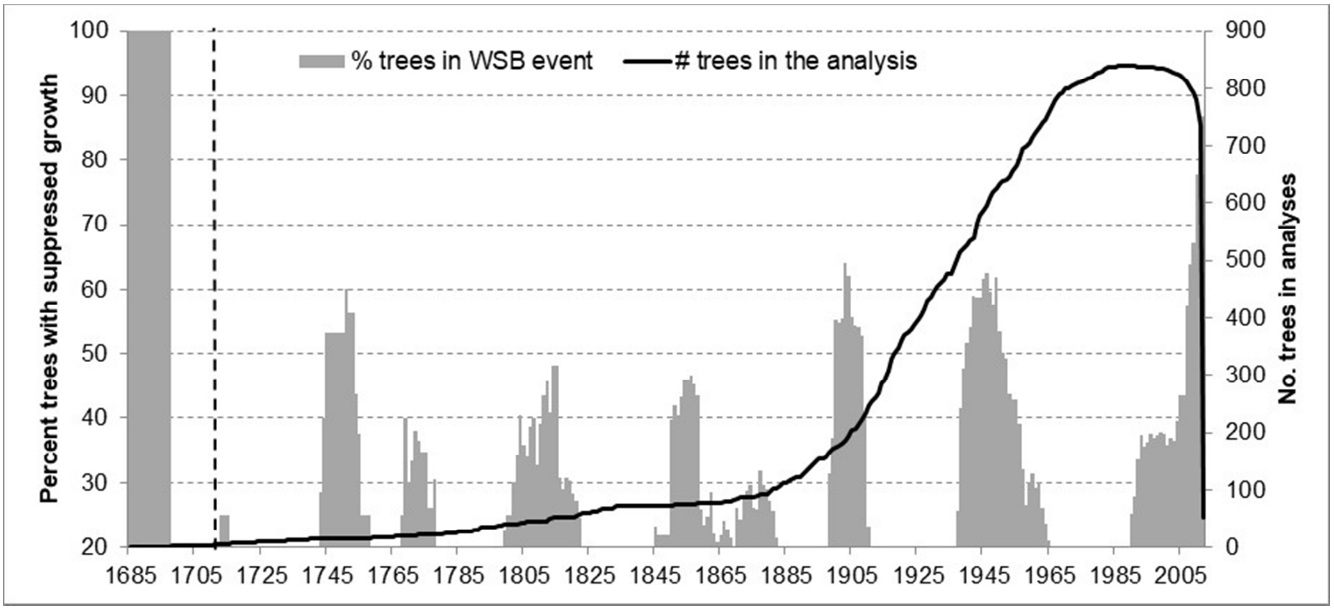


Figure 5. Consolidated outbreak chronology for southern B.C, with percent trees recording growth suppression from a WSB outbreak (primary y-axis). The solid line indicates the sample depth (number of trees in analyses in each year) (secondary y-axis). The vertical dashed line indicates the year above which there were more than 5 trees in the analyses (1716).

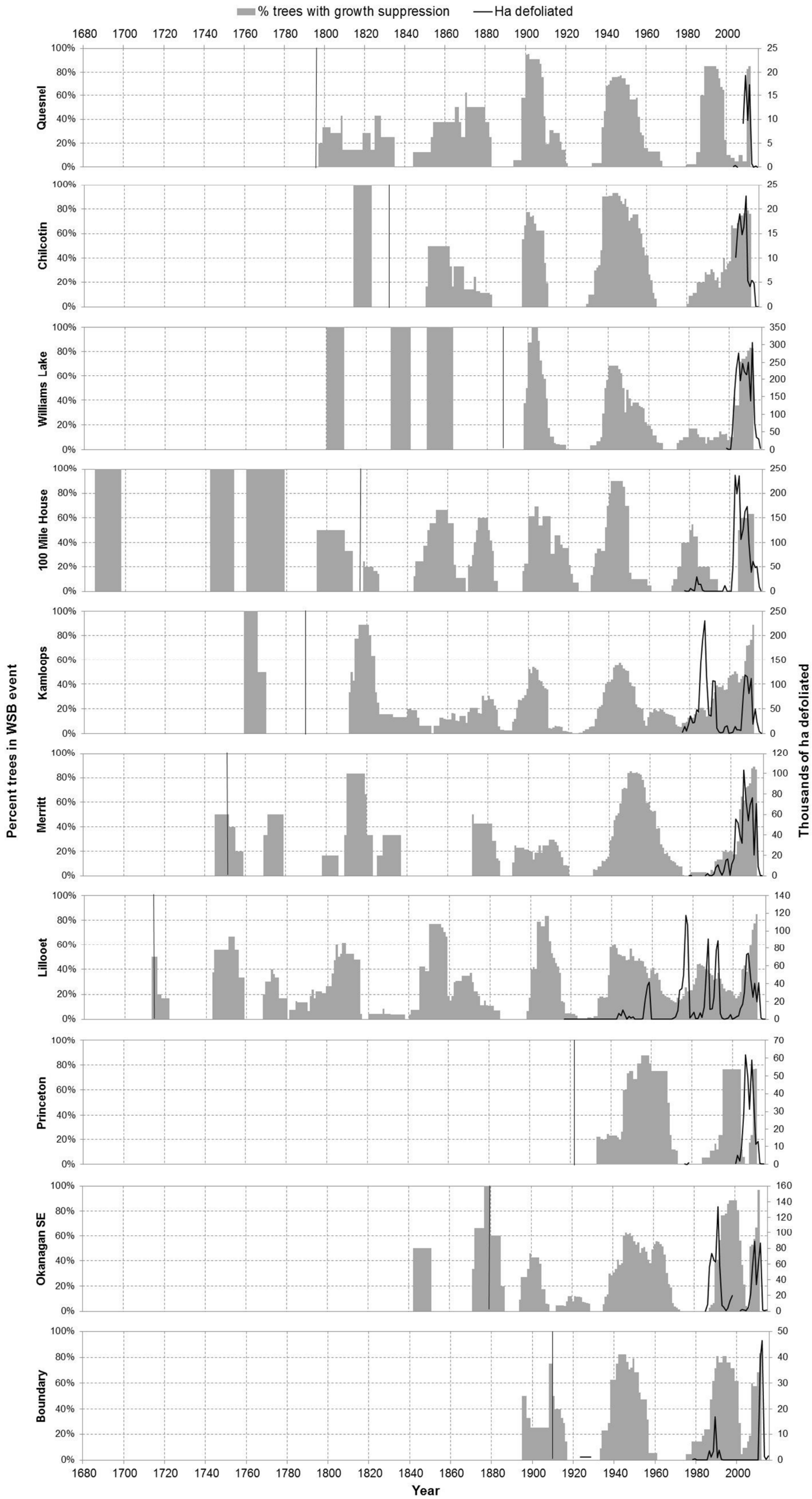

% trees with growth suppression
Ha defoliated
Quesnel
Chilcotin
Williams Lake
100 Mile House
Kamloops
Merritt
Lillooet
Princeton
Okanagan SE
Boundary
Percent trees in WSB event
Thousands of ha defoliated
Year

Figure 6. Frequency (percent trees) of radial growth suppression in Douglas-fir from 10 WSB Outbreak Regions (46 sites). Grey bars (primary y-axis) show relative frequency of Douglas-firs that were suppressed in each year from a WSB event and the black lines (secondary y-axis) show historical mapped defoliation in hectares for each year. The vertical black line represents the first year the sample depth was ≥5 trees.

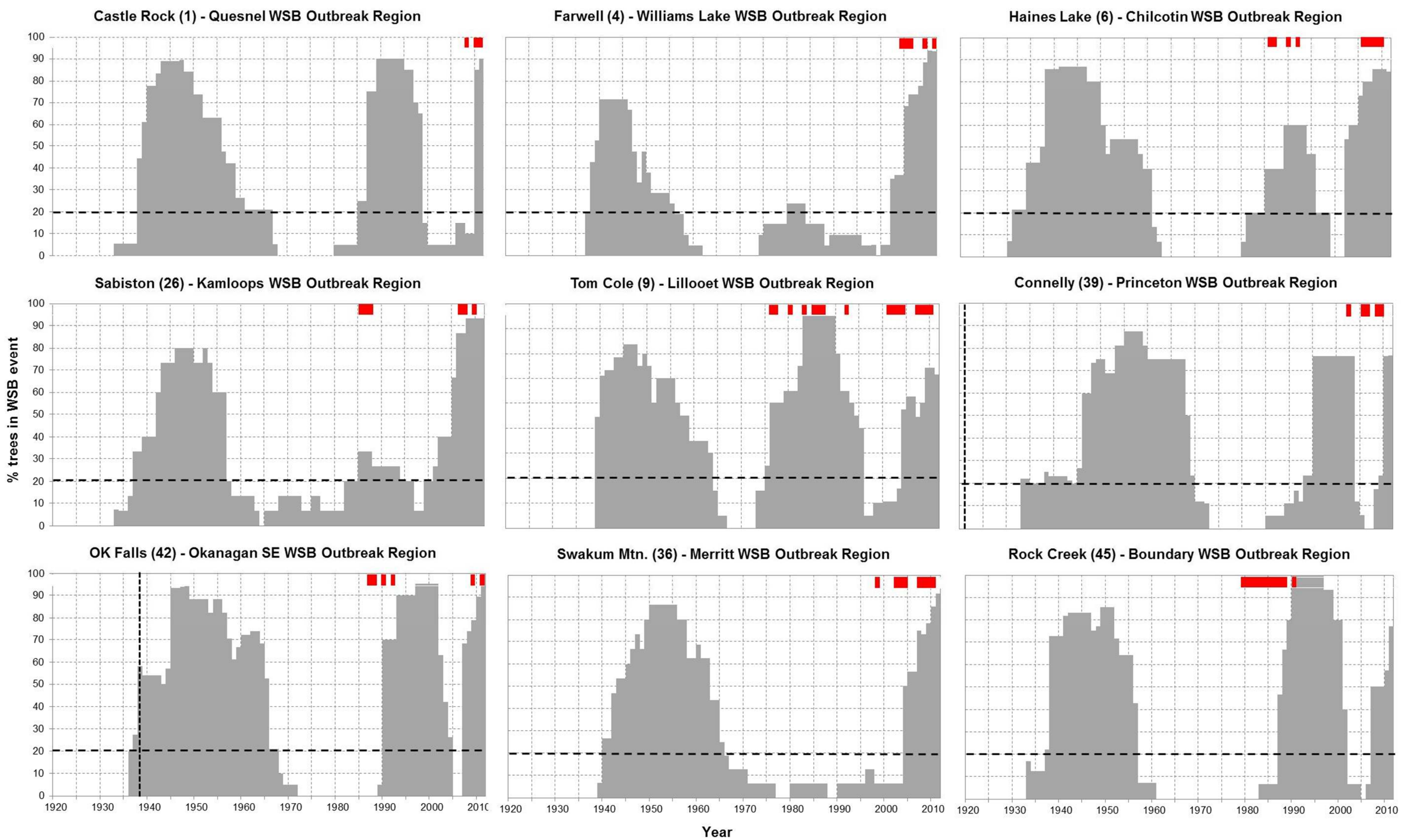

Castle Rock (1) - Quesnel WSB Outbreak Region
Farwell (4) - Williams Lake WSB Outbreak Region
Haines Lake (6) - Chilcotin WSB Outbreak Region
Sabiston (26) - Kamloops WSB Outbreak Region
Tom Cole (9) - Lillooet WSB Outbreak Region
Connelly (39) - Princeton WSB Outbreak Region
OK Falls (42) - Okanagan SE WSB Outbreak Region
Swakum Mtn. (36) - Merritt WSB Outbreak Region
Rock Creek (45) - Boundary WSB Outbreak Region
% trees in WSB event
Year

Figure 7. Percent trees (Douglas-fir) with radial growth suppression due to a WSB event at nine tree core collection sites and the year(s) defoliation was mapped. Grey bars show percent of Douglas-firs that were suppressed in each year and the red bars at the top of each graph indicate years when defoliation was mapped in the site. The dashed vertical line represents the first year the sample depth was ≥5 trees and the horizontal dashed line represents the recovery level when ≤20% of trees expressed growth suppression due to WSB feeding.