The effects of western spruce budworm (*Choristoneura occidentalis*) defoliation on Douglas-fir (*Pseudotsuga menziesii*): disturbance dynamics from the landscape to the cellular level

by

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B.Sc., University of Victoria, 2004
M.Sc., University of Regina, 2007

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Supervisory Committee

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Abstract

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The western spruce budworm (*Choristoneura occidentalis* Freeman) is the most widespread and destructive defoliator of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in British Columbia. Over the past two decades, western spruce budworm outbreaks have been sustained and widespread in the interior of British Columbia, leaving the forest industry and many forest-dependent communities increasingly vulnerable to the economic consequences of these outbreaks. While a great deal is known about the impact of western spruce budworm outbreaks on tree growth and form, substantial knowledge gaps remain as to the historic variability of western spruce budworm outbreaks and the consequences of defoliation on fundamental characteristics such as wood structure. This research focused on describing historic and contemporary western spruce budworm outbreaks across multiple spatial and temporal scales in south-central British Columbia using dendrochronology and wood anatomy techniques.

Outbreak histories over the past 435 years were reconstructed using a network of tree-ring chronologies from central British Columbia, revealing that 12 western spruce budworm outbreaks have occurred since the early 1600s, with a mean return interval of 30 years. Further, the research illustrates that outbreaks observed over the last 40 years are not unprecedented, which does not support the perception that western spruce budworm is moving northward into central British Columbia.

To evaluate the effects of a single western spruce budworm outbreak on the anatomical characteristics of Douglas-fir stemwood, tree ring data was collected from permanent sample plots that sustained both periodic and chronic western spruce budworm feeding. In mature even-aged stands of Douglas-fir, a documented outbreak occurred from 1976 to 1980 in the coastal transition zone of southern British Columbia. Based on microscopic wood anatomical measurements it was shown that the tree rings formed during this outbreak had significantly lower percentages of latewood, reduced mean cell wall thickness and smaller radial cell diameters relative to wood formed during periods without budworm feeding. Western spruce budworm defoliation temporarily modified cellular characteristics, which has implications for wood quality.

In uneven-aged stands of mature Douglas-fir, located in the xeric southern interior of British Columbia, there has been a sustained western spruce budworm outbreak since 1997. Tree rings formed during this outbreak had progressively larger earlywood lumen area and radial cell diameter, reduced latewood cell wall thickness, latewood radial cell diameters, and lower percent latewood. Mixed-effects models revealed that climatic variables, defoliation severity, defoliation duration, and in limited cases canopy class were the best predictors of xylem features. The severity and duration of western spruce budworm defoliation, as well as site factors that influence moisture conditions effect the degree and direction of anatomical changes in the stemwood of Douglas-fir.

This research fills a number of knowledge gaps by providing insights into the temporal and spatial dynamics of western spruce budworm outbreaks in central British Columbia over multiple centuries, and the plasticity of anatomical features in the stemwood of Douglas-fir during discrete western spruce budworm outbreaks. These research findings suggest that Douglas-fir forests are resilient to western spruce budworm outbreaks over space and time.

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List of Abbreviations

AIC	Akaike information criteria
AC	Autocorrelation
B.C.	British Columbia
BEC	Biogeoclimatic Ecosystem Classification
CC	Canopy Class
CD	Co-dominant
CUM	Cumulative Defoliation
CWT	Cell wall thickness
DBH	Diameter-at-breast height
D	Dominant
EW	Earlywood
FET	Fettes Defoliation
FIDS	Forest Insect and Disease Surveys
IDF	Interior Douglas-fir zone
I	Intermediate
ITRDB	International Tree Ring Database
LMEs	Linear mixed effects models
LA	Lumen area
LW	Latewood
MFI	Mean fire interval
PSP	Permanent sample plot
RCD	Radial cell diameter
REML	Restricted Estimation Maximum-Likelihood
WSB	Western spruce budworm

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Dedication

For Peter

Chapter 1 Forest Disturbances

1.1 Introduction

Forest ecosystems are complex systems, with a range of scales encompassed by ecological processes, functions and interactions (Holling 1992, Levin 1992, Peterson et al. 1998, Kerkhoff and Enquist 2007, Puettmann et al. 2013). Disturbances, relatively discrete events that change stand structure, resource availability, and/or the physical environment (White and Pickett 1985), are one of the principal mechanisms that shape forest ecosystems (White 1979, Oliver 1980, Agee 1993). Key attributes of disturbances include: type (e.g., insect outbreak, fire), spatial and temporal characteristics, magnitude, and interactions with other disturbances (White et al. 1999). Forests are often affected by disturbances through complex feedback loops. For example, climate strongly mediates the frequency and severity of disturbances, whether biotic or abiotic, which can impact forest composition and structure. In turn, forests influence climate through carbon sequestration and storage, and complex physical, chemical, and biological processes that can be strongly affected by disturbance regimes (Fettig et al. 2013). Finally, forest structure and composition influence the type and severity of disturbances, and the subsequent recovery and resilience of forest ecosystems post-disturbance (DeRose and Long 2014).

Though the term ‘forest health’ is imprecise, value-laden, and normative (O’Laughlin and Cook 2003, Sulak and Huntsinger 2012), it provides context to evaluate the role of disturbance agents in ecosystem level processes (Kolb et al. 1994). The Dictionary of Forestry defines forest health as a “*perceived condition of a forest derived from concerns about age, structure, composition, function, vigor, the presence of unusual levels of insects or disease, and resilience to disturbance.*” (Helms 1998: http://www.dictionaryofforestry.org/) Alfaro et al. (2010: page 115) suggest that a “*healthy forest can be considered one in which the underlying ecological processes of its ecosystems operate so that, on any temporal or spatial scale, they are resilient to the* *historical disturbance regime with which it evolved.*" Forest health definitions are closely linked to individual and cultural perspectives, land management objectives, and how spatial and temporal scales influence people's perceptions and interpretations (Kolb et al. 1994, Helms 1998, Sulak and Huntsinger 2012).

The term resilience is often used in conjunction with forest health. Resilience is defined as the magnitude of disturbance that a system can experience before it shifts into a different state, with different controls on structure and function (Holling 1973, Holling and Gunderson 2002). Resilience has the following properties: the amount of change a system can undergo and retain the same controls and function; the degree a system is capable of self-organization; and, the degree to which a system can build capacity to learn and adapt (Carpenter et al. 2001), a central idea of adaptive capacity (Gunderson 2000). Therefore, resilient ecosystems are those that persist even when disturbances lead to recombination's of evolved structures, renewal, and the emergence of new trajectories (Holling and Gunderson 2002, Folke 2006). Resistance, defined as the ability of a system to withstand disturbance and remain more-or-less the same is an important aspect of resilience (Grimm and Wissel 1997). A conceptual framework that explicitly differentiates resilience and resistance in silviculture was proposed by DeRose and Long (2014). Existing definitions were focused at appropriate scales: resistance is how vegetation influences disturbance behaviour; resilience is how disturbance influences the structure and function of an ecosystem. Clear management goals to build resistance or resilience at different scales create systems where management objectives can be set and outcomes measured (DeRose and Long 2014). Using this framework for a western spruce budworm (*Choristoneura occidentalis* Freeman; WSB) outbreak, a stand would be resistant (or made resistant) if tree species composition and/or structural traits reduced the severity of budworm feeding; the stand is resilient when structurally and functionally it is intact after the outbreak subsides.

Insects coexist in complex relationships with plant communities (Schowalter 2011), and their roles as disturbance agents are important for understanding ecosystem structure and function (Schowalter 1981). For insects that have outbreaks, population changes can be described by five distinct phases: 1) endemic phase - low population levels are maintained between outbreaks; 2) release threshold - the beginning of the outbreak cycle, where reproductive success results in partial escape from normal regulatory factors such as predation; 3) release phase - relatively high survival and continued population growth, and the rate of emigration peaks; 4) peak population – the population reaches its highest level but at a slower rate as resources become limiting, and predators and pathogens respond to increased prey/host density; and, 5) population decline – abundance decreases from multiple factors such as limiting resources, competition, predators and pathogens, which causes the population to return to the endemic phase (Schowalter 2011, and references therein). It is clear that the change from endemic to outbreak populations levels relies on numerous factors and their interactions, including climate cycles, weather, predator and parasite levels, host susceptibility and food quality (Schowalter et al. 1986, Wallner 1987, Berryman 1996, Raffa et al. 2008). Further, insects that are highly responsive to variations in weather are classified as eruptive (Wallner 1987, and references therein).

Insect outbreaks can be the most important disturbance agent in a forest, particularly where there are long intervals between stand-replacing events, such as fire or harvesting (Schowalter et al. 1997). Numerous studies have demonstrated that forests are resilient to, and recover from, insect outbreaks (e.g., Romme et al. 1986, Swetnam and Lynch 1993, Ryerson et al. 2003, Sibold et al. 2007, Diskin et al. 2011, Temperli et al. 2014, Alfaro et al. 2015). However, the consequences of climate change are likely to result in increased disturbance from a variety of agents including insects, disease, fire, and drought (Spittlehouse 2008, Allen et al. 2015). Climate directly influences insect survival, development, reproduction, dispersal and geographic distribution (Dale et al. 2001, Alfaro et al. 2010). It is highly likely that climate change will intensify outbreak behaviour of a number of bark beetle and Lepidopteran species (Logan et al. 2003), and that insects will adapt to new environmental conditions more quickly than their long-lived hosts (Logan et al. 2003, Volney and Hirsch 2005, Battisti 2008). For example, as temperatures continue to increase, insect outbreaks are expected to intensify in severity, frequency and spatial distribution (Dale et al. 2001, Alfaro et al. 2010). Temperate forests are becoming increasingly vulnerable to mortality and widespread die-back events (Allen et al. 2010, McDowell et al. 2011, Fettig et al. 2013, Allen et al. 2015), including more frequent and hotter droughts, and intensified insect outbreaks that could destabilize ecosystem resilience at multiple spatial scales.

1.2 Research motivation

Insect herbivores influence every major North American forest type. In western North America, the WSB (Lepidoptera: Tortricidae) is the most widespread and destructive defoliator of coniferous forests (Furniss and Carolin 1977, Fellin and Dewey 1982), and can seriously impact susceptible stands and landscapes (Alfaro et al. 1982, Alfaro and Maclauchlan 1992, Hadley and Veblen 1993, Volney 1994, Mason et al. 1997, Maclauchlan and Brooks 2009). Recently, Razowsky (2008) proposed revising the *Choristoneura occidentalis* nomenclature to *C. freemanni*, as use of *C. occidentalis* for a South African species had precedence (Razowski 2008). This revision has not been widely adopted, so I will use *C. occidentalis* (Freeman 1967) to refer to WSB.

In British Columbia (B.C.) the WSB has a long co-existence with its primary host tree, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Fig. 1.1) (Alfaro et al. 1982, 1985, Campbell et al. 2006, Alfaro et al. 2014). The interior Douglas-fir biogeoclimatic zone (Meidinger and Pojar 1991) is the most affected area in the province, having the greatest consecutive years of defoliation (Maclauchlan and Brooks 2009) and 1 million hectares mapped of historical budworm defoliation (Maclauchlan et al. 2006). The B.C. forest industry and forest-dependent communities are increasingly vulnerable to climate-related risks such as changes in species ranges and increased severity of insect outbreaks (Walker and Sydenysmith 2008). Over the last two decades sustained WSB outbreaks have been commonplace in many B.C. forests, especially in the dry interior (Maclauchlan et al. 2006). These outbreaks are a challenge economically and socially given the increasingly important resource role that Douglas-fir plays following the recent outbreak of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), which resulted in the mortality of over 710 million m^3 of timber in the province (BCMFLRNO 2012).

1.2.1 Research objectives

Natural disturbances are an integral part of the processes shaping and maintaining forested landscapes in B.C. Long-term information on the historic variability of WSB outbreaks is not available for several geographic regions of the province, and no research has addressed if, or how, WSB effects fundamental processes of wood formation and structure. Two goals of my dissertation research were to: 1) explore WSB outbreaks across multiple spatial and temporal scales using dendrochronology; and 2) examine the effects of WSB outbreaks from the novel perspective of quantitative wood anatomy, evaluating earlywood and latewood tracheid cellular characteristics at the microscopic level. The specific research objectives were to:

1. Develop multi-century reconstructions of WSB outbreaks across the Cariboo Forest Region of central B.C. using tree rings. Reconstructions were analyzed to determine the frequency and duration of outbreaks, the degree of regional outbreak synchrony, and the periodicity of outbreaks across multiple centuries.
2. Examine the effects of an eruptive WSB outbreak on even-aged coastal Douglas-fir in southwestern B.C. Cellular characteristics were analyzed at the inter-annual level in the stemwood to determine if crown defoliation impacted xylem elements.
3. Evaluate how stand structure, climate, and chronic WSB defoliation severity, and duration impact annual xylem elements and cellular characteristics of mature uneven-aged interior Douglas-fir stemwood.

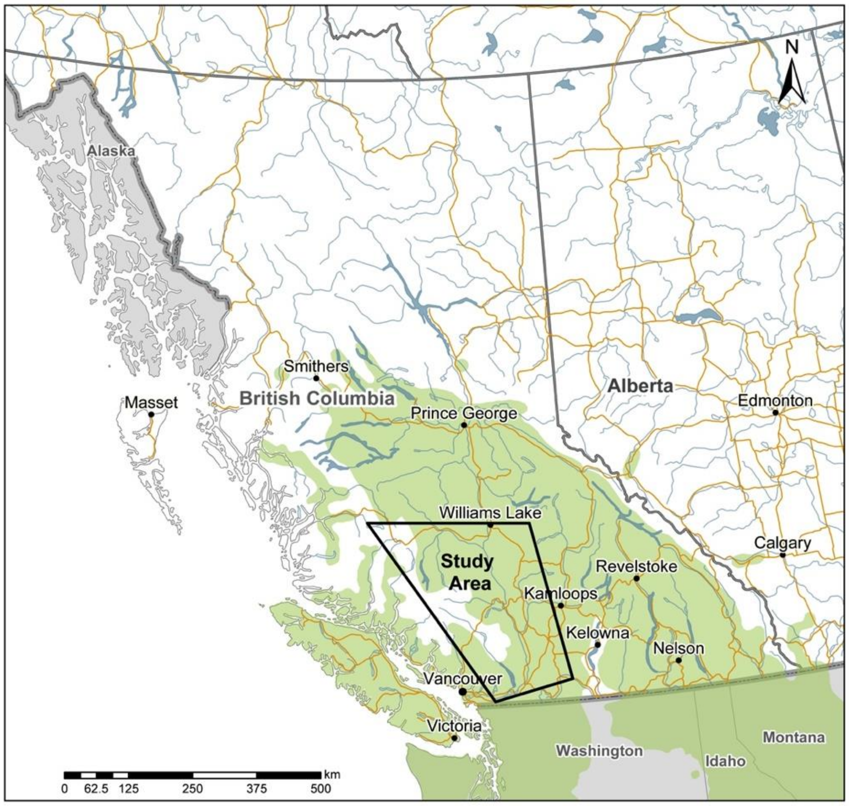

Figure 1.1 The range of Douglas-fir in western North America British Columbia, western Alberta and the northwestern United States (Little 1971), and the approximate boundaries of the study area used in this thesis.

1.3 Organization of the thesis

Following this chapter, Chapter 2 provides a detailed review of Douglas-fir ecology and WSB biology and outbreak dynamics. I also review WSB impacts, periodicity and synchrony across its range in western North America. Chapters 3, 4, and 5 contain the main results of the thesis, and were written as manuscripts for journal submission. Chapters 3 and 4 appear as published research papers in Forest Ecology and Management (Axelson et al. 2015) and Trees (Axelson et al. 2014), respectively. Chapter 3 presents new reconstructions of WSB outbreaks in the Cariboo Forest Region in the central interior of B.C. This research contributes to the understanding of outbreak frequency, duration and periodicity over 400 years at the northern limit of known WSB outbreaks. Chapter 4 is a case study in the B.C. coastal-transitional zone, and presents an analysis of the impact of WSB defoliation on the cellular characteristics of stemwood in mature even-aged coastal Douglas-fir forests. Chapter 5 presents a linear mixed modeling approach to evaluating climate and WSB defoliation severity and duration on the cellular characteristics of stemwood in uneven-aged interior Douglas-fir forests. Chapters 4 and 5 represent a novel approach using quantitative wood anatomy to explore the effect of WSB defoliation on xylem properties. The dissertation concludes with Chapter 6 where the results of this research are linked to the concepts of resilience and adaptive forest management. Appendix I has supplementary information relevant to Chapters 4 and 5, including examples of composite micro sections from each site, and summary tables for each stand with the average and standard deviation for earlywood and latewood tracheid variables, and sample depth for each year of the analyses.

Chapter 2 Douglas-fir and the Western Spruce Budworm

2.1 Douglas-fir

2.1.1 Range and ecology

Douglas-fir (*Pseudotsuga*) in the family Pinaceae has been a major component of western North America forests since the middle-Pleistocene (Lavender and Hermann 2014, and references therein). The native range is limited to western North America, Mexico, and eastern Asia, and includes 8 to 12 species, two of which are indigenous to the United States and Canada (Lavender and Hermann 2014, and references therein). The coastal variety (*P. menziesii* var. *menziesii* (Mirb.) Franco) grows on the moist Pacific slopes from British Columbia to California and is one of the most commercially important tree species on the coast. The interior variety (*P. menziesii* var. *glauca* (Beissn.) Franco) grows in the dry interior ranges of western North America from north-central B.C. to the mountains of central Mexico (Burns and Honkala 1990). Together these varieties have a vast north – south range spanning over 5000 km or 20 degrees of latitude, and extending from the Pacific coast to the eastern slopes of the Rocky Mountains (Burns and Honkala 1990). Douglas-fir is a long lived species: the coastal variety can easily exceed 700 years, while the interior variety was thought to rarely grow older than 400 years (Lavender and Hermann 2014, and references therein), this has been proven incorrect with one of the oldest interior Douglas-firs having a pith date of 1062 in New Mexico (Swetnam and Brown 1992). Coastal Douglas-fir reaches greater height, diameter, and volume than the interior variety, while interior Douglas-fir tends to be slower-growing, more cold hardy, more drought hardy, and more susceptible to Swiss needle cast (*Phaeocryptopus gaeumannii* (Rohde) Petrak) than coastal Douglas-fir (Lavender and Hermann 2014, and references therein).

Douglas-fir is well adapted to almost any moist, well-drained forest habitat below subapline zones within its range. In general, Douglas-fir will give way to mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), subalpine fir (*Abies lasiocarpa* (Hook.)

Nutt.), Engelmann spruce (*Picea engelmannii* Parry), western white pine (*Pinus monticola* Dougl.), and lodgepole pine at high elevations or more northerly latitudes. In moisture stressed environments Douglas-fir gives way to drought-tolerant species such as ponderosa pine and Garry oak (*Quercus garryana* ex Hook.). In areas that are very wet or poorly drained western redcedar (*Thuja plicata* Donn), and broadleaf species such as maples and alders (*Acer* and *Alnus* spp.) dominate. In the cool fog belt, associated with tidal zones of the Pacific coastal region, Douglas-fir gives way to Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (Silen 1978, and references therein).

2.1.2 Life cycle

Douglas-fir is monoecious with determinate growth after its first year (Lavender and Hermann 2014). Annual growth patterns in Douglas-fir are typical of determinate gymnosperms: the first stage is characterized by a period of bud break and active shoot elongation of the pre-formed initials from about late March to mid-August; the second stage is characterized by a period of dormancy, which includes bud set, and lasts from around mid-August until March of the following year. Seasonal growth begins in advance of bud burst when dormant buds begin to expand and initiate lateral buds in early April (Owens 1968, Allen and Owens 1972). Considerable lateral bud enlargement and bud-scale initiation and development occur in the vegetative bud before it bursts, which generally occurs in mid-May (Owens 1968). As vegetative bud burst becomes shoot elongation, which generally lasts until late June, lateral buds enlarge and develop along the shoot, developing into: a) an aborted bud that disappears after initiation; b) a partially formed undetermined latent bud; c) a vegetative bud; d) a pistillate bud; or, e) a staminate bud (Allen and Owens 1972, Owens and Molder 1973). Buds are completely formed by October to November and become dormant in early December when physiological activity is greatly reduced (Allen and Owens 1972). Douglas-fir generally initiates dormancy in response to environmental conditions in August, such as dry soils, which are a major trigger of dormancy (Lavender and Hermann 2014, and references therein).

After winter dormancy, lateral buds formed in the previous year become recognizable as either vegetative shoots or cones (Allen and Owens 1972). Douglas-fir is similar to other conifers where bud position and hormone concentrations characterize the differentiation of buds into staminate or pistillate cones. Pistillate buds develop in distal regions of the shoot where higher auxin concentrations would be expected, and staminate buds develop in more proximal regions that might have an auxin/gibberellin balance more favourable for pollen development (Owens 1969). Staminate buds begin to develop around late February and by the end of March pollen is mature and the cone has enlarged enough to push the bud scales apart. Mature Douglas-fir pollen has a smooth surface, and unlike the pollen of many other conifers lacks wing-like structures (Owens and Molder 1971). After staminate cone elongation is complete the cones hang downwards, dry out, and fall from the tree mainly by wind. The lack of wing-like structure and large size limits most pollen dispersal to 5-10 times the tree height, though reasonably strong winds may carry pollen several kilometers (Owens 1973).

Pistillate buds also begin to develop in late February, enlarging throughout the spring. By June cones are around 3 cm long, in an upright position with bracts bending outwards ready for pollination. When pollination is complete, seed cone orientation changes to a downward position, where they continue to enlarge throughout July while fertilization is underway. The final phase of the maturation occurs when the cones dry out, and ovuliferous scales open to release mature seed in September to October (Allen and Owens 1972, Owens 1973).

During the 17-month reproductive cycle, Douglas-fir phenology differs between coastal and interior varieties. The interior variety begins bud development before the coastal variety, ends shoot elongation and becomes dormant about four weeks ahead of the coastal variety. Fielder and Owens (1989) suggest this is a genetically fixed response to environmental cues in order to avoid late summer moisture deficits and the short frost-free season of a continental climate. While phenology differs between the two varieties, no morphological differences could be distinguished between pollen from coastal and interior varieties (Owens and Simpson 1986).

2.1.3 Seed production and tree establishment

Douglas-fir does not generally produce cones before the ages of 5 to 12 years (Allen 1942). Cone crops in Douglas-fir are cyclic but highly variable; a good-to-heavy cone crop occurs every 5 years but can vary between 2 and 7 years (Allen and Owens 1972). Heavy cone crops in one year are carried to the next, depressing subsequent cone crops (Owens 1969), and reducing the growth of shoots and roots (Silen 1978, and references therein). Cone production is highly variable from year-to-year even at small spatial scales (e.g., Owens 1973, El-Kassaby and Barclay 1992). In excellent years 2,000 to 3,000 cones per tree may be produced, while in a poor to fair year nearly all of the seeds produced may be lost to insects, birds and/or mammal herbivory (Hedlin 1964, Owens 1973). The high variability in cone production arises from a combination of factors, including the variation in the numbers of primordial floral buds or their subsequent losses, induced latency of immature buds, winter killing of developed buds, freezing of undeveloped cones, moisture stress, high light intensity (potentially interacting with high temperatures), and nutrient availability as carbohydrates, starch reserve, and certain amino acids are required for cone development (Allen and Owens 1972, Silen 1978, Lavender and Hermann 2014, and references therein). As the production of pollen and seed cones is metabolically expensive for Douglas-fir, when resources are limited trade-offs between growth and reproduction occur. In years with good cone crops relatively poor vegetative growth occurs (e.g., reduced annual ring increment), while the opposite occurs in years without cone crops (El-Kassaby and Barclay 1992).

Highly variable cone production in Douglas-fir is a major deterrent to natural regeneration in Douglas-fir (Campbell 1979, Burns and Honkala 1990). Germination of Douglas-fir is based on episodic colonization in extremely heterogeneous environments to which seedlings must have adaptive responses (Campbell 1979). Seeds germinate in the spring, which in warmer areas of its range occurs from mid-March to early April, and in the cooler parts of its range occurs as late as mid-May (Burns and Honkala 1990). Seedling growth in the first year is slow and is mainly limited by moisture, which triggers dormancy in midsummer that lasts until April or May of the following year (Burns and Honkala 1990). Seedlings of the coastal variety are most successful when they germinate on moist mineral soil or a light litter layer, while interior Douglas-fir seedlings require a duff layer for successful germination. Seedlings are relatively shade tolerant (Silen 1978) but do not do well with high competition from herbs and grasses. Regeneration, therefore, tends to be most reliable after wildfire destroys the seed source of competing vegetation (Burns and Honkala 1990). Less than half of seedlings survive beyond three years, culled by numerous factors, including: heat injury, drought, frost, and herbivory, which are influenced by microclimate factors such as shade, soil color, soil organic matter, and micro-topographic position (Campbell 1979, and references therein).

2.1.4 Disturbance dynamics

A number of insects feed on Douglas-fir seedlings and saplings, however it is primarily the conifer seedling weevil (*Steremnius carinatus* Boheman*)* and black army cutworm (*Actebia fennica* Tausher) that produce major damage (Lavender and Hermann 2014). The conifer seedling weevil, found mainly along the Pacific coast but also in wet-belt forests of interior B.C., commonly feeds on bark at ground level and can girdle seedlings and saplings. Girdling results in growth losses or mortality, however, the conifer seedling weevil is generally only a problem when ground cover has been removed by fire or harvesting practices (Koot 1972). The black army cutworm is found throughout B.C. and in its adult stage is particularly attracted to recently burned areas. When larvae emerge in the spring damage to coniferous seedlings and saplings can be very high, especially if its preferred food sources (e.g., herbaceous and shrub layers) are unavailable. Severe defoliation can result in seedling mortality or deformity, however the black army cutworm rarely causes significant damage for more than one or two seasons (Shepherd et al. 1992).

Prior to European colonization, disturbances in mature Douglas-fir forests were primarily from fire, windthrow, bark beetles (e.g., *Dendroctonus* spp.), defoliators (e.g., WSB and Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough), and fungal pathogens (e.g., *Phaeocryptopus gaeumannii* T. Rhode, *Armillaria ostoyae* (Romagnesi) Herink.). This variety of agents created a wide variation in disturbance type, frequency and severity across the range of Douglas-fir (Wong et al. 2003, Klenner et al. 2008, Simard 2009, Lavender and Hermann 2014, and references therein).

Wildfire was a major natural disturbance agent in forests across B.C. (Wong et al. 2003) until fire suppression was implemented in the mid-19th century. In lodgepole pine dominated systems in B.C. there has been a decreasing trend of area burned between 1920 and 2002 (Taylor et al. 2006). In the interior Douglas-fir zone there have been dramatic decreases in fire frequency over the last century (Wong et al. 2003, Klenner et al. 2008, and references therein). Fire severities range at the extremes from low: surface fires that burn litter, duff, loose woody debris on the forest floor, and undergrowth vegetation to high: fires that cause high or complete mortality of overstory trees, and are often stand-replacing (mixed severity fires are defined by a broad range of conditions between low and high extremes (Bradley et al. 1992). In the Pacific Northwest, mean fire intervals (MFI) have been estimated between 200 to 400 years and were considered largely high-severity events (Lavender and Hermann 2014, and references therein). However, it has been found that forests in the Pacific region experience a range of fire conditions, from frequent low- and mixed-severity fires to infrequent high-severity fires (Hansen et al. 1991). For example, on the south coast of B.C., MFI around 90 years have been inferred from charcoal analysis of lake sediments over the last 1300 years (Lucas and Lacourse 2013). In southern B.C., in the interior Douglas-fir biogeoclimatic zone (Hope et al. 1991), MFI have been estimated between 5–50 years (Wong et al. 2003, and references therein), characterized by frequent low-to-mixed-severity fire regimes that maintained open forests with large, widely spaced, predominantly fire-tolerant trees, such as Douglas-fir, ponderosa pine and western larch (Klenner et at. 2008, Lavender and Herman 2014, and references therein). Widespread and highly effective wildfire exclusion has enabled regeneration to colonize and persist beneath the overstory of previously open forests, changing forest structure and susceptibility to other disturbance agents (Hessburg et al. 1994, Macluachlan and Brooks 2009, Lavender and Hermann 2014).

Disturbance by insects can have a range of impacts depending on the type and severity of the disturbance. Douglas-fir beetle (*Dendroctonus pseudostugae* Hopkins) preferentially select the largest trees and are tissue feeders that bore through the tree bark and mine the phloem resulting in tree mortality. In an endemic phase, tree mortality tends to be widely scattered with a diffuse impact at the landscape level. Epidemics of Douglas-fir beetle are almost always associated with disturbances such as fire or windthrow that allow populations to build rapidly, killing 100s to 1000s of mature Douglas-fir, including healthy trees, across the landscape (Furniss and Carolin 1977). Douglas-fir beetle disturbances initiate canopy gaps that range from small areas where a few trees are killed to areas that are hundreds of hectares depending on the severity of the outbreak. This in turn creates openings for regeneration, especially of shade-intolerant species. Unlike bark beetles, defoliators such as WSB (see section 2.2.4) and Douglas-fir tussock moth are not limited by the size of their preferred hosts, Douglas-fir and true firs (*Abies* spp.) (Furniss and Carolin 1977). While overstory mortality is uncommon during WSB outbreaks, it can reach up to 40% during Douglas-fir tussock moth outbreaks (Hessburg et al. 1994), which develop rapidly and result in nearly complete tree defoliation when populations are high (Furniss and Carolin 1977, Wickman et al. 1981).

Disturbance interactions, whether between insect species, insect-disease complexes, or forest management practices, have important implications for resilience of Douglas-fir forests. Douglas-fir ecosystems have been highly modified by fire exclusion/suppression and harvesting, such as diameter-limited cutting that removed the largest trees (Smith 1962). Widespread removal of large trees has modified the diameter distributions of many forests, especially in the interior ranges. Harvesting, combined with fire exclusion, has skewed diameter distributions of stands towards densely spaced understory trees, which can lead to disturbance feedbacks and/or interactions. For example, in the Pacific Northwest repeated outbreaks of WSB and Douglas-fir tussock moth have increased stand susceptibility to bark beetles, such as Douglas-fir beetle and fir engravers (*Scolytus* spp.), which in turn can increase their susceptibility to both Armillaria root disease and laminated root rot (*Phellinus weirii* (Murr.) Gilbertson) (Hesseburg et al. 1994). The increasing availability of preferred host trees and changes in forest structure, such as increased vertical stratification of the canopy and more spatially continuous forests, creates a feedback loop that enhances insect population dynamics, which in turn can stress host trees making them more susceptible to other disturbances (e.g., Hessburg et al. 1994, Maclauchlan and Brooks 2009, Simard 2009).

2.2 Western spruce budworm

2.2.1 Introduction

A number of conifer-feeding species in the genus *Choristoneura* (Lepidoptera: Tortricidae) are native to Canada including spruce budworm (*C. fumiferana* Clemens), western spruce budworm (*C. occidentalis* Freeman), 2-year cycle budworm (*C. biennis* Freeman) and jack pine budworm (*C. pinus pinus* Freeman), and inhabit most of Canada's major conifer forest regions. Disturbances by this group are seen as a major threat to forest resources, resulting in a large amount of research on these species (Nealis 2015). Conifer feeding budworms are closely related species, sharing phylogenetic constraints that characterize their evolutionary histories and related adaptive strategies. The ecological relationships that arise from their adaptive strategies determine macro-ecological phenomena, such as eruptive population cycles (Nealis 2015). These budworms as a group are relatively specialised, feeding on one or only a few tree species within the single plant family Pinaceae. With their nearly identical life histories, and nearly indistinguishable mitochondrial DNA (Lumley and Sperling 2011) the most reliable method for differentiating these species is based on their geographic location and host-tree associations (Nealis 2015, and references therein).

2.2.2 Life cycle and ecology

The WSB is the most widespread and destructive defoliator of coniferous forests in western North America (Fellin and Dewey 1982, Volney and Fleming 2007), and outbreaks periodically throughout its range. The main hosts for WSB are Douglas-fir and true firs, though they may also feed on spruce (*Picea* spp.) and larch (*Larix* spp.) when they co-occur with their primary hosts (Furniss and Carolin 1977, Fellin and Dewey 1982, Harris et al. 1985). WSB is univoltine with obligate diapause in the field. In the interior of B.C., moths are active from mid-July to September, depending on elevation and the year (Nealis 2012). Eggs are laid in masses on host needles and hatch within two weeks. Neonate larvae do not feed but disperse to protected niches throughout the tree where they establish hibernaculae, moult to a second instar, enter diapause and overwinter. Time of emergence of second instar larvae in the spring varies from late April to June depending on weather, and larvae may emerge several days to weeks in advance of host tree budburst (Nealis and Nault 2005).

When budworms emerge in the spring they disperse extensively throughout the host canopy and mine old needles and feed on pollen cones (if available) until new buds swell and burst. During this period of advance foraging, substantial losses to the WSB population can occur (Nealis 2012, and references therein). WSB almost exclusively feed on new foliage; the period during which there is high nutritional quality in new foliage is extremely brief, therefore budworms are motivated to start the feeding season as early as possible as their survival and fecundity are reduced as the quality of current-year foliage rapidly declines (Nealis 2015, and references therein). During the feeding period larvae moult through five instars, which takes 30 to 40 days, and then pupate anywhere from late June to mid-August. Modeling with BioSIM10 has revealed that the phenology of WSB varies considerably with topography and regional climates. Across southern B.C. the peak 4th larval instar was modeled to occur anywhere from the first week of May to late July, with nearly as much variation at much smaller geographical scales (Nealis and Régnière 2013). Following approximately a 10-day pupation phase, adults emerge and mate, and females oviposit eggs and then die within 7-10 days (Furniss and Carolin 1977, Fellin and Dewey 1982, Nealis 2012, Nealis and Régnière 2013).

2.2.3 Population dynamics

Forest disturbances resulting from insect outbreaks occur when population oscillations are amplified to the point where insect densities have a measurable impact on the structure and/or function of the dominant elements of a forest ecosystem. Population densities of forest insects is determined by the ecological relationships among host plants, the herbivorous insects, and their natural enemies, in a "tritrophic" system (Cooke et al. 2007). In the tritrophic system key components interact to modulate population densities, however, their relative importance may change between outbreak cycles. Top down controls on insect populations arise from predatory and parasitic relationships, while bottom up controls result from the host and environmental conditions associated with the food source of the insect population. Migration to areas of low density is another important feature of outbreaking insects, and dispersal by adult spruce budworms can significantly augment local population densities via deposition of egg masses and resultant emergence of high numbers of larvae (Shepherd 1977, Wallner 1987). Global-scale climatic variability and regional-scale weather can exert strong density-independent influences on populations by determining the distribution of insects and their hosts, and on the population directly through effects on mortality and fecundity (Wallner 1987).

Top down effects on budworm populations arise from the influence of predators and parasites. There are around 40 species of insect parasitoids (these are insects that act like parasites but, unlike true parasites ultimately kill the host) that feed on WSB larvae (Furniss and Carolin 1977), including species in the Ichneumonidae and Braconidae (Hymenoptera), and Tachinidae and Sarcophagidae (Diptera) families (Furniss and Carolin 1977, Berryman 1996). Royama (1984) considered the combined action of parasitoids and diseases to be the main mechanism behind periodic oscillation of ~35 years in spruce budworm dynamics in New Brunswick. However, the associations between generalist natural enemies that are common to all budworms suggest that enemies in the budworm system respond to, rather than determine, the population density of budworms. Parasitoids are thought to follow changes in their prey (Berryman 1996) but these relationships tend to emerge near transition points in the outbreak cycle, and strong top down control is associated with already collapsing or endemic populations (Nealis 2015, and references therein).

Outbreaks of forest defoliating insects are commonly associated with species that feed early in the spring during rapid growth of host foliage, an adaptation that targets nitrogen quantity and and that avoids the inevitable decline in host foliage quality as the season progresses (Nealis 2012, and references therein). As Douglas-fir foliage matures through the growing season there are increases of foliar sugar, calcium and magnesium, and concomitant decreases in nitrogen, potassium, phosphorus and zinc (Clancy 1992). The seasonal period of host suitability defines a phenological window and there is strong selective pressure for WSB populations to be synchronized with bud phenology. Synchrony in the insect-host system is especially important to population densities because asynchrony in host bud pheonology and early-stage larvae, whom are ready and need to forage, will result in high mortality (Nealis 2012, and references therein). The genetic variation among Douglas-fir trees leads to variaation budburst phenology, which is an important mechanism of resistance to WSB feeding (Chen et al. 2003). Thus host plant phenology, foliage quality and quantity are examples of bottom up controls on populations. In addition to these specific influences, the preferred host(s) needs to be widespread in order for an outbreak to be geographically extensive. Conversely, when and where preferred hosts are less available the population has to cope with suboptimal conditions (e.g., longer forage seeking periods and/or distance), which can in turn influence the dynamics of local populations (Cooke et al. 2007, and references therein).

The effects of climate and weather on insect outbreaks cannot be easily explained, and the mechanisms that lead to population increase or collapse are still unclear. In the budworm system, weather appears to modulate, rather than drive the rate of change in population densities at multiple scales, largely through its effect on ecological relationships that determine fecundity and survival (Nealis 2015). On a global scale, seasonal temperatures and rainfall patterns are major factors that determine the distribution of organisms, and through natural selection both insects and their hosts become extremely well adapted to these factors. Weather on the other-hand, such as spring temperatures, can have a range of direct or indirect effects on populations. Direct effects include mortality to overwintering stages due to density-dependent developmental lags, and selective mortality that shifts population genetics. Indirect effects include asynchrony between insects and their host resulting in mortality or conversely, synchronization of host flowering leading to increased larval survival (Wallner 1987, and references therein, Schowalter 2011).

2.2.4 Outbreak impacts

WSB outbreaks are considered to last from the first to the final year in which host trees sustain visible defoliation (Harris et al. 1985). During an outbreak, which typically lasts several years, defoliation causes reductions in annual radial growth (i.e., growth suppression), reductions in annual height growth and stem defects, regeneration delays and in the worst cases tree mortality (Shepherd et al. 1977, Alfaro et al. 1982, Van Sickle et al. 1983, Alfaro and Maclauchlan 1992, Hadley and Veblen 1993, Maclauchlan et al. 2006).

The impacts of WSB herbivory are characterized by a period of reduced growth caused by budworm feeding on current-year foliage, followed by a period during which trees recover their crown foliage (Alfaro et al. 1982). In the Southern Rocky Mountains of the U.S., Swetnam and Lynch (1989) reported periodic growth reductions between 21% and 24% and maximum growth reductions between 50% and 59% during WSB outbreaks. During a single 11-year outbreak in southwestern B.C., annual diameter losses averaged 65%, assuming growth during the outbreak period was equivalent to average pre- and post-infestation increments (Alfaro et al. 1982). Over the course of four outbreaks from the 1920s to the 1970s, growth reduction led to average cumulative volume (potential) losses of 17% (1926-34), 33% (1943-49), 37% (1956-1963) and 44% (1970-77) (Alfaro et al. 1985). In projections of growth and yield in uneven-aged stands of interior Douglas-fir, Alfaro and Maclauchlan (1992) modelled a 7-year outbreak and found that different outbreak intensities resulted in average volume reductions of 7% (light), 39% (moderate) and 52% (severe) over a 20-year annual increment window. The growth suppression response in Douglas-fir to WSB feeding is lagged in time between the initiation and cessation of defoliation. It has been found that growth loss initiation and cessation lag defoliation 1 to 3 years (Alfaro et al. 1982, Mason et al. 1997, Axelson et al. 2014). Alfaro et al. (1982) suggest that earlywood growth is dependent on older foliage, while latewood growth is dependent on new foliage; average growth occurs during the first year of defoliation as old foliage is unaffected, and a 1-year lag in growth reduction persists after feeding has ceased because of the cumulative loss of foliage due to consecutive years of feeding.

WSB outbreaks can affect height growth directly by killing the terminal bud and die-back of the uppermost portion of the stem (topkill); and indirectly through recovery responses such as the formation of crooks and forks, resulting in non-commercial future growth (Shepherd et al. 1977). Inspection of 65 stands in southwestern B.C. after a WSB outbreak revealed that 80% of stands had topkill, which affected 19% of the trees on average (Fiddick and Van Sickle 1979). In stands of coastal Douglas-fir, severe defoliation resulted in a 6-year period with no apical growth, representing ~6 m of lost potential height growth (Shepherd et al. 1977). Van Sickle et al. (1983) determined that no vertical growth took place for a number of years during an outbreak, and internodes were often missing for one or more years after conspicuous feeding had ceased. This suggests that recovery of height growth, like radial growth, is delayed beyond the active feeding period, which is likely due to carbohydrate limitations resulting from reduced photosynthesis during active budworm herbivory.

Understory trees can be the most severely defoliated trees in uneven-aged stands compared to other cohorts present in the forest (Maclauchlan and Brooks 2009). Severe defoliation leads to significant stem dieback (up to half of the total tree height) resulting in sustained periods of height growth suppression and slow recovery (Lorraine Maclauchlan *personal communication*). Slow recovery combined with stem defects negatively impacts merchantability of these understory trees, which in many managed forests are considered future crop trees (Van Sickle et al. 1983). Another consequence of sustained and/or severe defoliation is tree mortality, where understory trees withstand the highest mortality levels (Alfaro et al. 1982, Hadley and Veblen 1993, Maclauchlan and Brooks 2009). Alfaro et al. (1982) found that in southwestern B.C., defoliation severity was similar across the different size cohorts, however mortality was concentrated in the intermediate and suppressed trees (42-65%) and was related to cumulative defoliation of five or more years (Alfaro et al. 1982). In the Colorado Front Ranges, tree mortality was also concentrated in the understory cohort, however defoliation severity was also higher in younger stands with high densities (Hadley and Veblen 1993). In a study of over 800 plots in B.C., Maclauchlan and Brooks (2009) determined that understory trees were the most severely defoliated in all stand structure types, and that maximum consecutive years of defoliation and tree mortality were the highest in xeric-hot forest types in the interior Douglas-fir biogeoclimatic zone.

2.2.5 Outbreak periodicity and synchrony

In B.C. there have been six to eight widespread outbreaks of the WSB since 1909 (Maclauchlan et al. 2006). From the early 2000s there has been a continuous WSB outbreak across much of the province, and aerial surveys have mapped around 7 million hectares of cumulative defoliation. Maclauchlan et al. (2006) suggest that there are five distinct outbreak sub-regions in the southern interior of B.C. that are characterized by distinct outbreak periods that are not necessarily synchronized with adjacent areas. However, a major limitation to understanding how WSB outbreaks vary over space and time is the very short duration of systematically surveyed insect damage in B.C. While some Forest Insect and Disease Surveys (FIDS) records date to the early 1900s, standardized surveys did not begin in the province until the late 1940s (Harris et al. 1985). Tree ring reconstructions of WSB outbreak histories have significantly supplemented limited survey records, suggesting that outbreaks have occurred across the range of WSB for centuries (Alfaro et al. 1982, 1985, Anderson et al. 1987, Swetnam and

Lynch 1989, 1993, Swetnam et al. 1995, Ryerson et al. 2003, Campbell et al. 2005, 2006, Lynch 2012, Alfaro et al. 2014, Flower et al. 2014, Axelson et al. 2015). A number of these studies also illustrate that the return intervals and periodicity of reconstructed outbreaks align reasonably well, suggesting periodic behaviour of WSB outbreak cycles over time (Table 2.1).

Table 2.1 The return interval and periodic components of tree ring based reconstructions of western spruce budworm in western North America. Bold characters indicate strongest periodicities as discussed by authors.

Location	Return Interval[1]	Periodicity[2]	Authors
British Columbia			
Southern interior (Kamloops)	-	~ **30**, **43**, 70[a]	Campbell et al. (2006)
Southwestern (Pemberton to Okanagan)	26 - 37	~ 3, **19**, **24**, **33**[b]	Alfaro et al. (2014)
Central (Cariboo)	30 - 133	~ 16, **32**, 64[c]	Axelson et al. (2015)
United States			
Western Montana	32 - 35	-	Anderson et al. (1987)
Southern Rocky Mountains (Colorado and New Mexico)	33 - 43	-	Swetnam and Lynch (1989)
North-central New Mexico	-	~**20**, 33[a]	Swetnam and Lynch (1993)
Northeastern Oregon	27 - 47	-	Swetnam et al. (1995)
Southern Colorado	32 - 78	~ **25**, **37**, 83[a]	Ryerson et al. (2003)

[1] Return interval calculated as the duration of time between the start years of outbreaks

[2] Periods calculated based on time series analysis: [a] Singular Spectrum Analysis, [b] Multi-taper method, [c] Continuous wavelet transform

Across western North America, the return interval of reconstructed outbreaks ranges between 26 and 47 years. The longer intervals calculated in central B.C. (Axelson et al. 2015) and southern Colorado (Ryerson et al. 2003) (Table 2.1) were based on the minimum thresholds used to identify outbreaks, where authors used >75% and ≥50% of trees affected to distinguish higher severity outbreaks, respectively. If these two return periods are excluded from a global average, the return interval across all studies ranges from 28 to 40.5 year (± 8 years SD). This range is reasonably consistent with time series analysis of outbreak reconstructions, where the strongest periodicities identified in a number of studies ranges from 20 to 43 years (Table 2.1, and references therein). Nealis (2015) cautions that emphasis on mean values may reinforce the perception of the regularity of outbreak cycles, while there is actually variation in outbreak behaviour that contains relevant information for understanding outbreak dynamics.

Despite Nealis' (2015) caveat, periodic behaviour centered around 35-years has also been determined from numerous studies of spruce budworm outbreaks in eastern North America (e.g., Blais 1983, Royama 1984, Boulanger and Arseneault 2004, Boulanger et al. 2012), and like these outbreaks, WSB outbreaks become intermittently synchronized at regional to continental scales (Table 2.1; Hadley and Veblen 1993, Flower et al. 2014). For example, a reconstructed WSB outbreak in the early 1900s was a geographically widespread event across the central B.C. (Axelson et al. 2015), the southern interior of B.C. (Campbell et al. 2005, 2006, Alfaro et al. 2014), southern Vancouver Island (Harris et al. 1985), the Pacific Northwest in the U.S. (Flower et al. 2014) and northeastern Oregon (Swetnam et al. 1995). While this broadly synchronized outbreak is likely the exception rather than the rule, regional synchronization of outbreaks is a common feature of many outbreak reconstructions.

Cooke et al. (2007) suggest that population densities of forest insects are determined by the interactions of the tritrophic system, which are often lagged in space and time, generating periodic, high-amplitude fluctuations that can be synchronized over large geographical areas. The occurrence of large-amplitude cycles in forest Lepidoptera depends on the insect's environment and the ecological conditions to which the species is exposed, rather than the organism itself or its biological attributes (Berryman 1996). Defoliator outbreaks that have been synchronized over very large areas has led to research that examines mechanisms that entrain synchronous outbreaks in time and space (Royama 1984, Myers 1998, Williams and Liebhold 2000, Peltonen et al. 2002, Liebhold et al. 2004, Økland et al. 2005). Many insects that are classified as eruptive, such as WSB, are very responsive to variations in weather. Insect outbreaks can follow periods of drought or be influenced by combinations of drought and excessive moisture; temperature can have an array of direct or indirect effects on populations, such as mortality in overwintering larval stages, and synchronization of host and insect leading to increased larval survival, or alternatively asynchrony between host and insect with opposite results (Wallner 1987, and references therein). On southern Vancouver Island there were three documented WSB outbreaks between 1909 and 1930, afterwhich outbreaks have not ocurred (Harris et al. 1985). Thomson and Benton (2007) found that changes in climate have increased winter air temperature (January to mid-March), mediated by increased sea surface temperatures. Increased winter temperature has resulted in earlier larval emergence, but not earlier bud flush in Douglas-fir. The relationship between budburst phenology and WSB emergence is of critical improtance in the budworm system (Nealis 2012), and on southern Vancouver Island it appears that climate has decoupled the insect-host relationship resulting in a complete absence of WSB outbreaks in this region for over 70 years.

The Moran effect describes how synchronous exogenous factors, such as weather or climate, can synchronize population densities over large areas (Moran 1953). This effect was considered the dominant mechanism causing spatial synchrony in outbreaks of a number of Lepidoptera species across regional scales by Peltonen et al. (2004), while Williams and Liebhold (2000) found that synchronized spruce budworm outbreaks were driven by the combined effects of a regional weather patterns and the dispersal behaviour of the adults. Tree ring studies of WSB outbreaks and synchrony have focused on the Moran effect, as quantitative analysis is possible between tree ring records and climatic data. For reconstructions in the Southern Rocky Mountains in Colorado (Ryerson et al. 2003) and in Colorado and New Mexico (Swetnam and Lynch 1993) outbreaks were found to correspond with periods of normal to wet conditions. In the Pacific Northwest outbreak initiation coincided with periods of transitional climate, with warm-dry conditions occurring in the three years preceding outbreak initiation, and cool-wet conditions occurring during the first three years of an outbreak (Flower et al. 2014). In southern B.C., Campbell et al. (2006) found low winter precipitation at the beginning of the growing season was related to the occurrence of WSB outbreaks. Visual comparisons of regionally synchronous WSB outbreaks and climatic proxies for the central interior of B.C. indicate that the influence of climate on outbreak dynamics is highly complex, with the association of the variables not remaining temporally stable over time (Axelson et al. 2015, and references therein).

Several potential mechanisms synchronize outbreaks including correlated, large-scale weather-related perturbations; ecosystem elements driven by generally inefficient natural enemies and the abundance of host plants; and dispersal of moths (Liebhold et al. 2004, Cooke et al. 2007). At larger geographical scales the interplay between these elements can be a source of both spatial and temporal variability and moves ecosystems away from a precise and complete synchronization (Cooke et al. 2007). Of the several mechanisms that may cause synchrony, identifying which mechanism is more, or the most important, is difficult and thus the causes of population synchrony remain an elusive ecological question (Liebhold et al. 2004).

Chapter 3 Multi-century reconstruction of western spruce budworm outbreaks in central British Columbia, Canada

3.1 Article information

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3.1.2 Authors' contributions

J.A. developed the study and hypothesis, conducted field, laboratory work, and statistical testing, wrote the manuscript and produced all of the tables and figures. D.S. provided tree-ring chronologies archived at the University of Victoria Tree-Ring Laboratory, contributed to the Introduction, Methods sections and reviewed and edited the manuscript. L.D. provided tree-ring chronologies from archived material at the University of British Columbia tree-ring laboratory and reviewed and edited the manuscript. R.A. provided tree-ring chronologies available from archived at the Pacific

Forestry Centre, contributed to the Introduction, Methods sections, and reviewed and edited the manuscript.

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3.2 Abstract

The western spruce budworm (*Choristoneura occidentalis* Freeman; WSB) is a widespread and destructive defoliator of commercially important coniferous forests in western North America. In British Columbia, Canada, Douglas-fir (*Pseudotsuga menziesii*) is the most prevalent host, and records show that significant outbreaks have primarily occurred in the southern interior over the last century. In the central interior of British Columbia, particularly in the Cariboo Forest Region, the most recent outbreak of western spruce budworm, which is in its second decade, has been severe and widespread. It is perhaps due to this long outbreak, which is unprecedented in duration since detailed surveys began in the 1950s that there is an anecdotal perception that the western spruce budworm is expanding its range northward into the region, affecting Douglas-fir near the edge of its northern distribution. However, very little is known about the long-term outbreak history of western spruce budworm in the central interior of the province. In this study we used 11 Douglas-fir host chronologies and 2 regional *Pinus* non-host chronologies to reconstruct western spruce budworm outbreaks over a 435-year period. Standard dendrochronological techniques were used to develop tree-ring chronologies at each site and the program OUTBREAK was used to detect outbreak periods. We reconstructed 12 outbreaks starting in early 1600s with a mean return interval of 30 years. Sensitivity analysis illustrated that including light, moderate and severe intensity thresholds modified the number of reconstructed outbreaks, their duration and mean return interval. Sub-regional chronologies based on biogeoclimatic subzones and variants

(BEC units) revealed strong synchrony of some outbreak events, but not all. Wavelet analysis of the sub-regional chronologies demonstrated the quasi-periodic behavior of western spruce budworm over the entire record, which averaged 32 years. By reconstructing WSB dynamics over 400 years we demonstrated that outbreaks observed over the last 40 years in the Cariboo Forest Region are not unprecedented.

Keywords: Douglas-fir, western spruce budworm, outbreaks, species range, dendroecology, Cariboo Forest Region

3.3 Introduction

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

Since the early 1900s documented WSB outbreaks in the Douglas-fir forests of British Columbia (B.C.) has resulted in the defoliation of over 5.6 million hectares (Maclauchlan et al. 2006). Despite the fact that Douglas-fir is one of the most commercially valuable conifer species in B.C., attention to WSB outbreak dynamics has primarily been confined to the southern interior of the province (Harris et al. 1985, Maclauchlan et al. 2006) where tree ring studies show that over the last 500 years WSB outbreaks have occurred repeatedly, with a mean return interval of approximately 33 years (Campbell et al. 2006, Alfaro et al. 2014). Typically these outbreaks are demarcated in annual tree rings by periods of reduced incremental growth that last through the outbreak and a number of years following outbreak cessation (i.e., recovery period) (Alfaro et al. 1982).

Little is known about the long-term WSB disturbance history in the Cariboo Forest Region of central interior B.C. Systematic Forest Insect and Disease Surveys (FIDS), which began in the early 1950s, first documented WSB outbreaks in 1974 (Erikson 1992), and by the late 1990s over 200,000 hectares were experiencing moderate to severe defoliation (Westfall and Ebata 2001). Since that time, WSB defoliation has occurred episodically across the B.C. interior and in 2003 increased to encompass >500,000 hectares (Maclauchlan et al. 2006). Overlay analyses in the Thompson-Okanagan Forest Region, immediately south of the Cariboo Forest Region, suggests that defoliation since the 1980s is historically unprecedented in duration and extent (Maclauchlan et al. 2006).

The recent history of defoliation in the Thompson-Okanagan Forest Region suggests that WSB may be expanding its range northward into the Douglas-fir forests of the adjoining Cariboo Forest Region in response to ongoing climate change (Murdock et al. 2013). Given that WSB defoliation in this region would result in significant depletions in the assumed timber supply (BCMFR 2007, Woods et al. 2010), developing a comprehensive understanding of long-term forest-budworm interactions is essential for updating current forest management strategies (Shepherd 1994, BCMFR 1995).

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

3.4 Methods

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

3.4.1 Study area

The Cariboo Forest Region extends from 51°00' to 52°30' north latitude and from 120°30' to 125°45' west longitude in the B.C. central interior (Fig. 3.1). The Fraser Plateau makes up a large portion of the region and is characterized by a level to gently rolling landscape incised by river valleys, and local uplands with elevations predominantly ranging from 900 to 1500 metres above sea level (m asl). The Chilcotin Plateau extends along the western periphery of the region, beyond which the Coast Mountains rise sharply to elevations up to 4,000 m asl. This landscape configuration results in a strong rain shadow effect and the western Chilcotin is the driest portion of the study area, with annual precipitation at Tatla Lake averaging 403 mm/yr.

As Pacific air masses move further eastward towards Williams Lake, humidity levels and precipitation increase slightly, with annual precipitation totals averaging 417 mm/yr (Wang et al. 2012). Summer months are typically dry, with most precipitation resulting from numerous convective storms. In the winter months Arctic air masses result in extended periods of extreme cold temperatures (Steen and Coupé 1997).

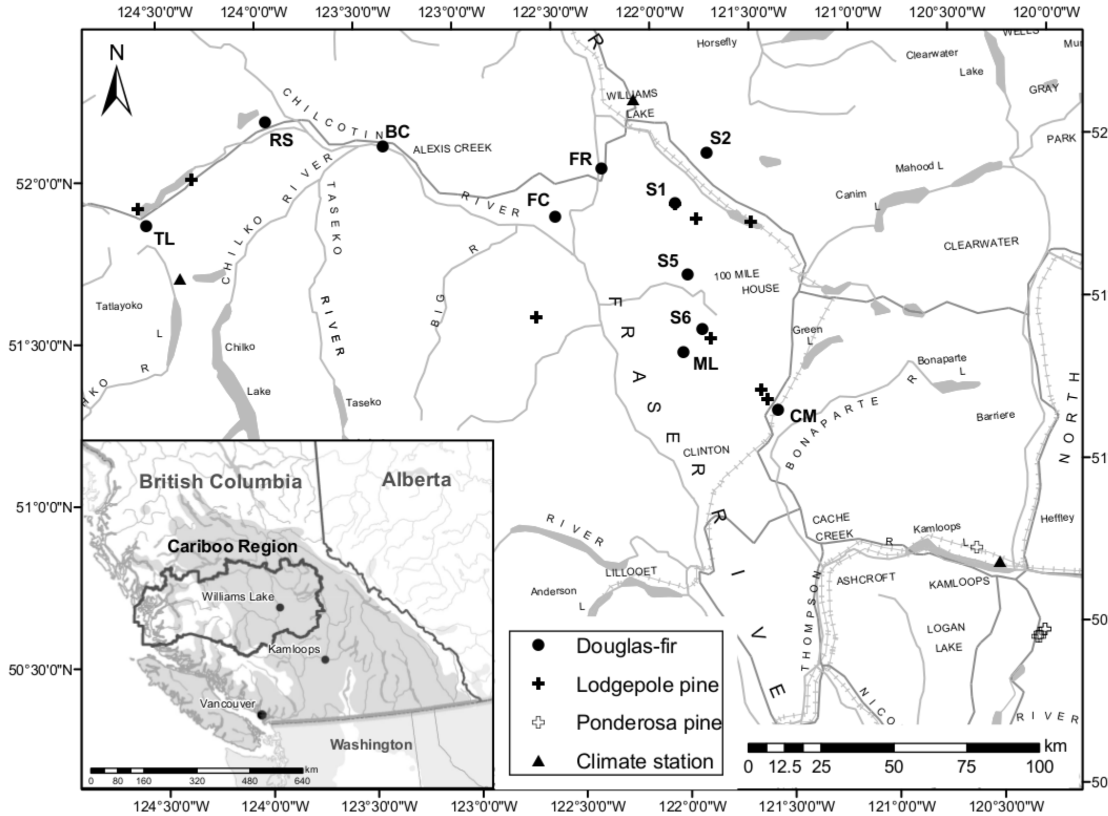

Figure 3.1 Location of western spruce budworm host (Douglas-fir) and non-host (pine species) tree ring chronologies and climate stations in the Cariboo Forest Region, British Columbia, Canada (*see* Table 3.1 for chronology abbreviations). Inset map shows the outline of the Cariboo Region and the range of Douglas-fir in grey shading (Little 1971).

In B.C. the biogeoclimatic ecosystem classification (BEC) uses vegetation, soils, and topography to identify geographic areas, referred to as biogeoclimatic zones, which have a relatively uniform climate. BEC zones are further divided into subzones based on the moisture and temperature regime of the area, respectively and some BEC subzones are further classified into variants based on their location or distribution within a subzone (Meidinger and Pojar 1991). In the Cariboo Forest Region, the Interior Douglas-fir (IDF) BEC zone makes up approximately 45% (17,000 km^2) of the area and is located above the valleys of the Fraser, Chilcotin, and Chilanko rivers (Steen and Coupé 1997). The very dry-warm (xw) and very dry-mild (xm) subzones are the driest and warmest in the region, and are transitional between grassland and forest (Table 3.2). The dry-cool (dk) subzone covers the largest area in the Cariboo Forest Region and is comprised of four variants, with the Chilcotin variant (dk4) being the coldest and driest (Steen and Coupé, 1997; Table 3.2). Herein, we shall refer to BEC subzones (e.g., xm) and BEC variants (e.g., dk4) simply as BEC units.

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

The negative radial growth correlations exhibited by all three tree species to summer temperature in interior B.C. suggests that increased evaporative losses and water stress during high temperature intervals are detrimental to tree growth (Watson and Luckman 2002). In mid- to low elevation interior ecosystems, tree ring variability is primarily related to factors affecting water supply, especially precipitation, indicating that tree growth is limited by moisture availability in the previous and current growing seasons (Watson and Luckman 2002, Campbell et al. 2006, Littell et al. 2008, Chen et al. 2010, Griesbauer and Green 2010, Lo et al. 2010, McLane et al. 2011).

3.4.2 Sample collection, preparation and outbreak detection

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

All host (Douglas-fir) and non-host (ponderosa pine and lodgepole pine) chronologies were developed by preferentially sampling the oldest appearing trees in the stand at breast height with 5.2 mm diameter increment borers, collecting two cores from a minimum of 20 trees. After air-drying, the cores were glued to slotted mounting boards and sanded to a fine polish (180 to 600 grit sandpaper) until individual tracheids within the annual rings were visible under the microscope. Tree ring-widths were measured using either WinDendro (Ver. 2009b, Regents Inc. 2009) or a Velmex uniSlide digitally encoded traversing table at a precision of 0.01 mm. The measured ring-width series from individual sites were visually crossdated and the list method was used to identify possible errors in measurement due to false or locally absent rings (Yamaguchi 1991). Crossdating was verified using the program COFECHA (Holmes 1986). Douglas-fir sites developed at locations less than 10 km apart were combined into a single chronology. Individual ponderosa pine and lodgepole pine sites were crossdated and then combined into species-specific regional non-host chronologies (Fig.3.1; Table 3.1). Tree-ring series were standardized to remove the biological and geometric growth trends using the program ARSTAN (Cook et al. 2007). In ARSTAN, user-defined curves were applied to each measurement series and a bi-weight robust mean was computed using a mean value function that minimized the effect of outliers, producing a dimensionless stationary index time series with a defined mean of 1.0 and a relatively constant variance (Cook and Kairiukstis 1990). The ring-width series were standardized using a two-step process: 1) a negative exponential curve that removed biological growth trends; and, 2) 50-year 50% frequency response cubic spline (Cook and Peters 1981).

The relationship between climatic variables (average temperature (°C) and total precipitation (mm)) and tree-growth of the host and non-host chronologies was evaluated using the *bootRes* package (Zang 2012) in R (R Core Development Team 2013), which computes Pearson correlation coefficients and uses bootstrapping to calculate significance and confidence intervals (Zang and Biondi 2012). Correlation coefficients were computed between residual chronologies and homogenized temperature (Vincent et al. 2012) and adjusted precipitation (Mekis and Vincent 2011) data from the Adjusted

Historical Canadian Climate Database (http://www.ec.gc.ca/dccha-ahccd/) for the Kamloops, Williams Lake and Tatlayoko Lake stations (Table 3.3). Correlation coefficients were computed on monthly climate variables from the previous June (*t-1*) to September of the current growing year (*t*) in order to determine the significance of the previous growth season climate on tree growth in the current year (Fritts 1976).

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

To evaluate the robustness of the reconstructed outbreak history we compared those occurring in the latter half of the 20th century with documented outbreaks in the southern interior of B.C. (Harris et al. 1985, Erikson 1992) and with those identified in recent provincial aerial overview surveys (Westfall and Ebata, 2001-2011). Our reconstructions were also compared to previous multi-century WSB outbreak reconstructions at sites in the southern B.C. interior (Campbell et al. 2005, 2006, Alfaro et al. 2014), and in the northwestern US (Swetnam et al. 1995, Flower et al. 2014).

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

While it was not the primary objective of this study, we examined possible relationships between synchronous outbreaks and climate by comparing the sub-regional chronologies with independently reconstructed summer temperature (June-August) and May 1 snow water equivalence (SWE) anomalies for the Tatlayoko Lake station (Table 3.3; Starheim et al. 2013). To facilitate comparison between the datasets, the reconstructed climatic anomalies were transformed using a 10-year spline. Synchronous WSB outbreaks were defined as periods when > 5 consecutive years had index values in the lowest 75% percentile in at least 3 of the 4 sub-regional chronologies.

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

Table 3.1 Properties of western spruce budworm host and non-host chronologies in the Cariboo Forest Region of British Columbia, Canada. Chronologies are arranged from east to west (Fraser River to Tatlayoko Lake) and from the north to south (Farwell Canyon to Chasm; Figure 3.1) of the study area.

Site Name	Site ID	Latitude	Longitude	Elevation (m asl)	Source[1]	BEC Units[2]	Series Length	No. dated series	Inter-series *r*	AC[3]
Host - Douglas-fir										
Fraser River	FR	51°59’34”	122°17’11”	670	2010-11	IDFxm	1585 - 2010	57	0.732	0.667
Bull Canyon	BC	52°05’20”	123°21’53”	760	2010-11	IDFxm-dk4	1560 - 2009	38	0.756	0.494
Redstone	RS	52°09’35”	123°54’08”	990	2010-11	IDFdk4	1385 - 2009	68	0.740	0.719
Tatlayoko Lake	TL	51°51’17”	124°36’23”	1048	2010-11	IDFdk4	1544 - 2010	59	0.683	0.788
Farwell Canyon	FC	51°50’53”	122°30’51”	898	2010-11	IDFxm	1490 - 2009	57	0.773	0.563
Site 1	SI	52°01’12”	121°45’0”	900	UBC	IDFdk3	1523 - 1994	42	0.855	0.774
Site 2	S2	51°52’12”	121°55’12”	1050	UBC	IDFdk3	1491 - 1995	43	0.739	0.734
Site 5	S5	51°39’0”	121°52’48”	1129	UBC	IDFdk3	1632 - 1995	31	0.796	0.742
Site 6	S6	51°28’48”	121°49’12”	1285	UBC	IDFdk3	1437 - 1994	40	0.804	0.762
Meadow Lake	ML	51°24’34”	121°55’43”	1171	2010-11	IDFdk3	1516 - 2010	50	0.766	0.665
Chasm	CM	51°12’25”	121°28’16”	1055	2010-11	IDFxw-dk3	1458 - 2010	71	0.738	0.719
Non-host										
Regional lodgepole pine	PL	51-52°	122-124°	985-1280	PFC, UBC	IDFdk - SBPSxc	1775 - 2011	233	0.544	0.813
Regional ponderosa pine	PY	50-52°	119-121°	700-1113	ITRTB , UBC, UVTRL	BGxw - PPxh	1576 - 2011	95	0.621	0.739

[1] Source: 2010-11-this study; ITRDB-International Tree-Ring Database; PFC-Alfaro et al. (2004); UBC-Daniels and Watson (2003); UVTRL-Campbell et al. (2005, 2006)

[2] Biogeoclimatic abbreviations: BG=Bunchgrass, IDF=Interior Douglas-fir, PP=Ponderosa pine; dk=dry-cool, xm=very dry-mild, xw=very dry-warm

[3] First order autocorrelation

Table 3.2 Characteristics of the biogeoclimatic units where chronologies were sampled. Adapted from Steen and Coupé (1997).

	Biogeoclimatic Units			
Interior Douglas-fir (IDF)	**xw**	**xm**	**dk3**	**dk4**
BEC unit label	Very Dry - Warm	Very Dry - Mild	Dry - Cool Fraser	Dry - Cool Chilcotin
Elevation (m asl)	600-1000	800-1200	750-1200	1050-1350
Area (km^2)	362	2,373	8,953	3,994
Location in Cariboo Forest Region	Southeast corner.	Valleys of the Fraser and Chilcotin rivers.	Southeast to northwest (Williams Lake), east of the Fraser River valley.	North and south of the Chilcotin and Chilanko river valleys.
Mean annual precipitation (mm)	No data	392	433	355
Mean annual temperature (°C)	3.5	4.0	3.3	2.8
General description	Open park like appearance, with mixed ponderosa pine and little to no regeneration.	Parkland of grasslands and Douglas-fir forests, some clumps of aspen.	Multi-aged Douglas-fir forests with abundant but clumpy regeneration.	Coldest variant of IDFdk subzone in province, lodgepole pine present where there is cold air accumulation.
Dominant herb layer	Pinegrass; Bluebunch wheatgrass	Pinegrass; Kinnikinnick	Pinegrass; Twinflower	Pinegrass; Kinnikinnick
Adjacent BEC zones[1]	Above PP	Above BG below IDFdk	Above the IDFxm and below SBPS/MS	Below SBPS

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

Table 3.3 Climate station name, ID number, period of record, location and elevation used in correlation analysis with tree-ring chronologies located across the central interior, B.C., Canada.

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

3.5 Results

3.5.1 Tree-ring data

The tree-ring chronologies used in this study were collected at sites found throughout the study area (Fig. 3.1). Fourteen archived and newly collected Douglas-fir chronologies sites were combined to develop 11 host chronologies (Table 3.1). Six archived lodgepole pine chronologies and six archived ponderosa pine chronologies were combined to develop two regional non-host chronologies (Table 3.1).

The Douglas-fir chronologies were constructed from trees found primarily in the dry-cool Fraser or the dry-cool Chilcotin BEC units, with the exception of the Fraser River and Farwell Canyon chronologies constructed from trees located in the very dry-mild BEC unit (Tables 3.1 and 3.2). Two chronologies were located in transitional BEC units: the Bull Canyon chronology is transitional between very dry-mild and dry-cool Chilcotin; in the southeast the Chasm chronology is transitional between the very dry-warm and dry-cool Fraser (Fig.3.1; Tables 3.1 and 3.2). All the Douglas-fir sites were characterized by open forests (averaging 375 trees per hectare) where the drier stands (very dry-mild and very dry-warm) represent a transition from grassland to more continuous forest at higher elevations (dry-cool BEC units) (Steen and Coupé 1997).

Douglas-fir sites were located on rolling to terraced terrain, predominantly on south to southwest facing slopes with elevations ranging from 600 to 1285 m asl (Table 3.1). The chronologies collected for this study (2010 and 2011) came from trees exhibiting current WSB defoliation, as well as evidence of previous outbreaks, such as topkill and sparsely foliated crowns.

The regional lodgepole pine chronology was compiled from sites located in the dry-cool Fraser or dry-cool Chilcotin BEC units or adjacent BEC units (e.g., Sub-Boreal Pine Spruce) (Table 3.1). Stands were composed predominately of lodgepole pine with minor components of veteran Douglas-fir and/or aspen (*Populus tremuloides* Michx.). Lodgepole pine stands typically had a higher density than the Douglas-fir sites (around 800 to 900 trees per hectare), and were located on mainly flat to rolling terrain with elevations ranging from 985 to 1280 m asl (Table 3.1).

The regional ponderosa pine chronology was compiled from sites in the southern portion of the study area, at the northern range of the species distribution (Burns and Honkala 1990), or from the adjacent Thompson-Okanagan Forest Region (Fig. 3.1). Stands were located in the Bunchgrass or Ponderosa pine BEC units, where the climate is characterized by warm to hot, dry summers and moderately cold witners with little snowfall (Steen and Coupé 1997). Ponderosa pine stands were mixed with Douglas-fir and characterized by open forests (averaging 270 trees per hectare) with the understory dominated by pinegrass (*Calamagrostis rubescens* Buckl.) located on slopes with variable aspects (Table 3.2).

3.5.2 Dendrochronological characteristics

The Douglas-fir trees sampled in this study averaged 494 years in age (Table 3.1), while the ponderosa and lodgepole pines ranged in age from 435 to 236 years, respectively (Table 3.1). Inter-serial correlation (*r*), the variation in tree ring growth among all sampled trees in a stand, ranged between 0.683 to 0.855 in Douglas-fir and from 0.544 to 0.621 in the non-host chronologies, demonstrating that all three species record a strong commonality in the response to environmental influences. First-order autocorrelation, common in tree-ring series describes the correlation between the tree ring width in the previous year (*t-1*) and ring width in the current year (*t*) (Fritts 1976). In Douglas-fir, the lag-1 autocorrelations ranged from 0.494 to 0.788 and the non-hosts were 0.739 to 0.813, indicating the strong influence of radial growth in the previous year growth on current year's growth (Table 3.1).

Pearson correlation coefficients between residual chronologies and mean temperature and total precipitation indicate that both host and non-host radial growth was similarly affected by climate (Table 3.4). The most consistent significant correlations in all of the chronologies occurred for previous August precipitation (*t-1*) and, to a lesser extent, previous June precipitation (Table 3.4). Significant correlations to mean monthly temperatures tended to be sporadic and no strong pattern emerged across sites (Table 3.4).

3.5.3 Outbreak reconstructions

Initially we developed two sets of outbreak reconstructions: one was constructed using the regional lodgepole pine chronology as the non-host; and, a second was constructed using the regional ponderosa pine chronology as the non-host. The average correlation coefficient between the reconstructions was 0.60 (ranging from 0.42 to 0.83) (Fig. 3.2a), indicating good correspondence between non-hosts and providing confidence that either could be used in the outbreak analyses. The outbreak reconstructions for each non-host are plotted for Site 5 (Fig. 3.2b), which had an average correlation coefficient between reconstructions of $r = 0.58$, illustrating that overall the two non-hosts produced similar outbreak histories in terms of timing and duration. The most significant difference between the two reconstructions was the outbreak intensity. Reconstructions based on lodgepole pine generally had a higher ratio of trees meeting the outbreak parameters than those based on ponderosa pine (e.g., Fig. 3.2b). This pattern was consistent for all sites suggesting that WSB outbreak reconstructions based on ponderosa pine are likely to be more conservative. Nonetheless, we chose to use only the regional ponderosa pine chronology to construct our final WSB reconstruction as it extended further back in time (> 400 years).

Our WSB reconstructions show that outbreaks have occurred in the Cariboo Forest Region for the past 300 to 400 years (Fig. 3.3). These outbreaks have varied in intensity and duration at individual sites, but at times were highly synchronous across the study area (Figs. 3.3 and 3.5). The sites with the longest outbreak reconstructions (FR, RS, FC, S6, ML and CM; Table 3.1) all recorded outbreaks in the early 1600s and 1630s, where 80 to 100% of trees recorded outbreaks (Fig. 3.3). From the 1650s to the early 1700s site-specific outbreaks occurred at generally low levels. In the 1720s a synchronous, moderate outbreak occurred at all sites (Fig. 3.3). In the 1770s a high intensity (60-80% of trees) outbreak occurred at nearly all the sites, with the exception of FC and S1 (Fig. 3.3). The 1800s were characterized by a period of predominately stand-specific outbreaks of variable intensity until the late 1800s when all the sites recoded a severe outbreak (80-100% of trees) (Fig. 3.3).

Our reconstructed outbreak history was compared with survey records from the 20th and 21st centuries. Ninety-one percent of the Douglas-fir stands examined in this study record outbreaks from the late 1930s to mid-1940s (Fig. 3.3). Although few records exist in the study area prior to 1994, documented outbreaks in the mid-1930s to mid-1940s to the south and west closely coincide to our reconstructed outbreaks (Harris et al. 1985). The 1974 WSB outbreak observed by Erikson (1992) near the FC site chronology (Fig. 3.1) appears at 64% of our sites, albeit as a low intensity event that impacted from 20-40% of the trees at sites recording the outbreak (Fig. 3.3). All of the sites recorded outbreaks in the mid-1990s (Fig. 3.3), and by the mid-2000s 80 to 100% of trees at all sites recorded the outbreak events mapped by the provincial aerial overview survey (Westfall and Ebata 2001-2011).

Table 3.4 Significant Pearson correlation coefficients ($p<0.05$) between current residual tree-ring chronologies and climate variables in the growth seasons prior to (*italics*) and concurrent with ring formation.

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

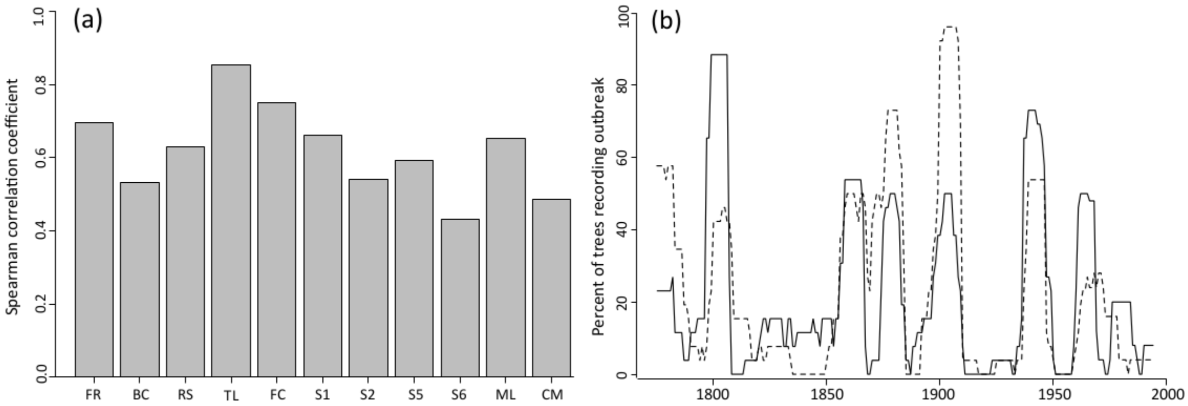

Figure 3.2 (a) Pairwise Pearson correlation coefficients between reconstructions of western spruce budworm outbreaks computed using the regional non-host lodgepole pine chronology (PL) and the regional non-host ponderosa pine chronology (PY); All correlations are significant (p<0.05) (b) An example of western spruce budworm reconstructions for Site 5 (S5) using PL (solid line) and PY (dashed line).

Table 3.5 summarizes the reconstructed outbreak history by number, duration and return interval for light, moderate and severe defoliation periods. The greatest number of outbreaks corresponded to light defoliation, and the least to severe defoliation events. In the light defoliation category we reconstructed an average of 12 outbreaks with an average duration of 15 years (± 1.8 years) and a return interval of 29.8 years (± 5.6 years) (Table 3.5). For moderate defoliation there was an average of 5 outbreaks with an average duration of 11 years (± 5.5 years) and return interval of 64.2 years (± 20.2 years). Under the severe defoliation category there was an average of 2 outbreaks, with an average duration of 9.6 years (± 1 year) and a return interval of 132.8 years (± 44.5 years) (Table 3.5).

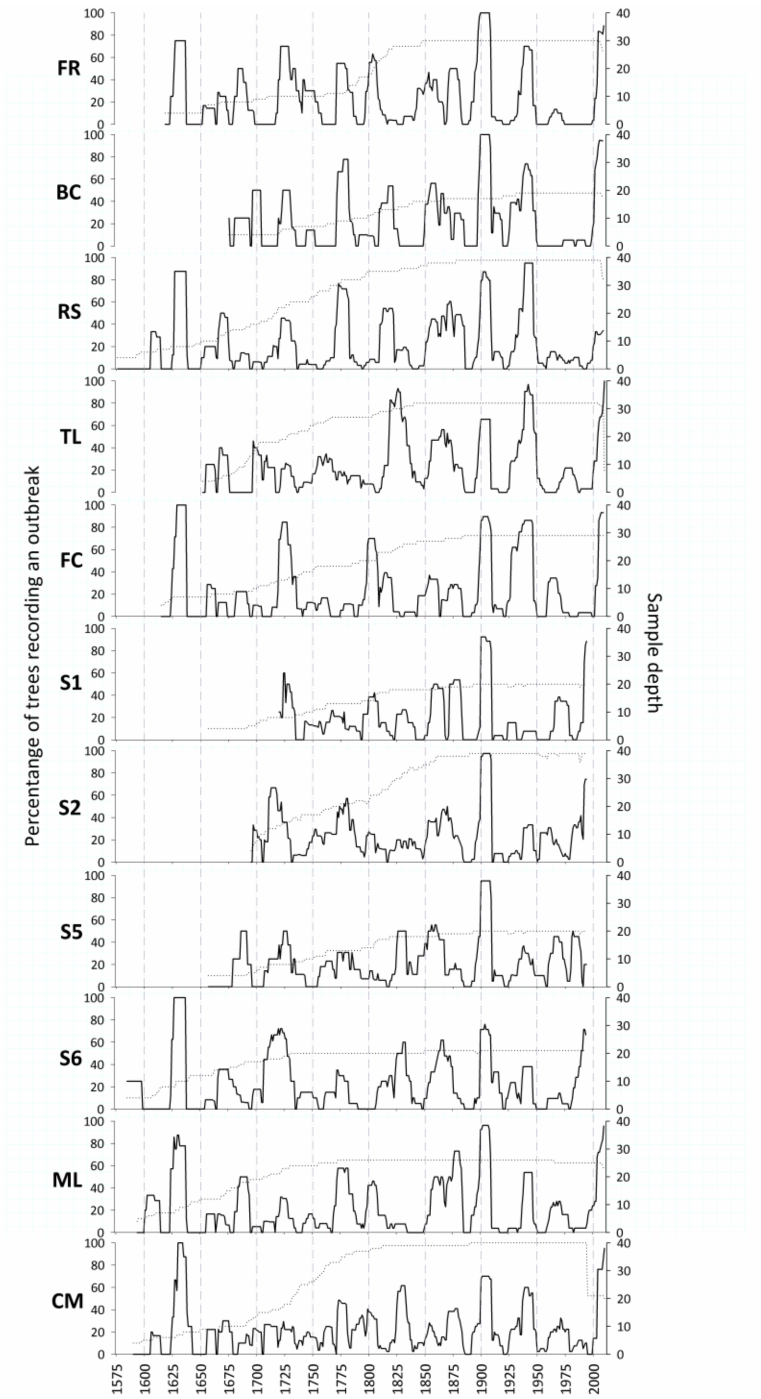

Figure 3.3 Reconstructions of western spruce budworm outbreaks across the Cariboo Forest Region, British Columbia, Canada. Outbreak reconstructions were truncated to a minimum sample depth of four trees. Left y-axis is the percentage of trees recording an outbreak; right y-axis sample depth for each site.

3.5.4 Outbreaks and climate

From 1658 to 2009, smoothed records of Tatlayoko Lake summer temperature (June-August) and May 1 snow water equivalence (SWE) highlight the low frequency variability inherent to each time series (Figs. 3.5a and 3.5b). Positive summer temperature anomalies are generally accompanied by negative May 1 SWE anomalies (and vice versa), although this strong inverse relationship weakens in the 1840s until the late 1880s, when the amplitude of anomalies flattens (Figs. 3.5a and 3.5b). The decreased amplitude in the summer temperature record is particularly notable and lasts from around the mid-1700s to late 1800s (Fig. 3.5a). From 1658 to 2009, ten synchronous outbreak periods at the sub-regional scale were identified (Fig. 3.5c). In general, synchronous outbreaks at the beginning and end of the record correspond to positive summer temperature and negative SWE anomalies (Fig. 3.5). However, the opposite trend occurs from the late 1700s to the 1850s and late 1920s when synchronous outbreaks corresponded to negative temperature and positive SWE anomalies. From the early 1800s to the 1860s there is an absence of synchronous outbreaks in sub-regional chronologies and decomposition in a common signal between chronologies (Fig. 3.5c), which corresponds to decreased amplitude in summer temperature anomalies over the same period (Fig. 3.5)

3.5.5 Periodicity of outbreaks

Wavelet analysis revealed both high and low frequency variability in the WSB sub-regional chronologies (Fig. 3.6). The high frequency ~16-year period is apparent in each sub-regional chronology primarily from the 1670s to approximately the late 1700s to early 1800s. This mode of variability appears associated with high frequency oscillations in the sub-regional chronologies, which is most pronounced in the dry river valley sites of the very-dry mild BEC unit, and is nearly absent in the wetter forests of the dry-cool Fraser unit (Fig. 3.6; Table 3.2). The low-frequency, multi-decadal signal centered on the 32-year period is a prominent feature in all of the sub-regional

Table 3.5 Reconstructed number, duration and return interval of outbreaks by individual sites organized by their sub-regional biogeoclimatic unit grouping. Return intervals are given for three levels of budworm outbreak intensity.

				Duration (years)		Return Interval[3] (years)	
Site	Start of record[1]	Percent of trees affected (%)[2]	No. of outbreaks	Mean	SD	Mean	SD
Very Dry – Mild (xm)							
FR	1619	15	10	18	12	38	21
		50	9	11	10	42	22
		75	2	11	1	189	115
FC	1615	15	11	14	6	34	7
		50	5	13	4	76	28
		75	4	10	3	94	61
Dry – Cool Chilcotin (dk4)							
BC	1676	15	9	16	6	35	19
		50	7	8	2	44	11
		75	2	8	4	113	13
RS	1576	15	13	14	8	30	15
		50	6	27	43	61	48
		75	3	9	2	156	165
TL	1652	15	12	15	9	29	13
		50	4	11	5	47	14
		75	2	9	1	95	35
Dry – Cool Fraser (dk3)							
S1	1720	15	11	12	5	21	8
		50	4	8	3	67	56
		75	1	10	-	93	-
S2	1695	15	11	17	13	28	18
		50	3	9	4	94	28
		75	1	10	-	-	-
S5	1657	15	11	15	6	27	14
		50	5	7	2	54	33
		75	1	10	-	-	-

Site	Start of record[1]	Percent of trees affected (%)[2]	No. of outbreaks	Duration (years)		Interval[3] (years)	
				Mean	SD	Mean	SD
S6	1585	15	12	16	8	33	14
		50	5	11	5	73	35
		75	1	11	-	-	-
Very Dry – Warm (xw)							
ML	1594	15	12	16	12	33	19
		50	7	9	3	54	29
		75	2	10	1	190	117
CM	1590	15	19	13	6	20	9
		50	4	9	2	94	72
		75	1	8	-	-	-
Average	1634	15	12	15.1	1.8	29.8	5.6
		50	5	11.2	5.5	64.2	20.2
		75	2	9.6	1.0	132.8	44.5

[1] Start of record for each site truncated when there were fewer than four host trees in the sample

[2] Percent of trees equates to defoliation intensity: low >15%, moderate >50% and severe >75%

[3] Return intervals are number of years between start year of outbreaks

Table 3.6 Pairwise Pearson correlation coefficients (p<0.001) between corrected chronologies. For each chronology the highest between-sites correlation coefficient is outlined.

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

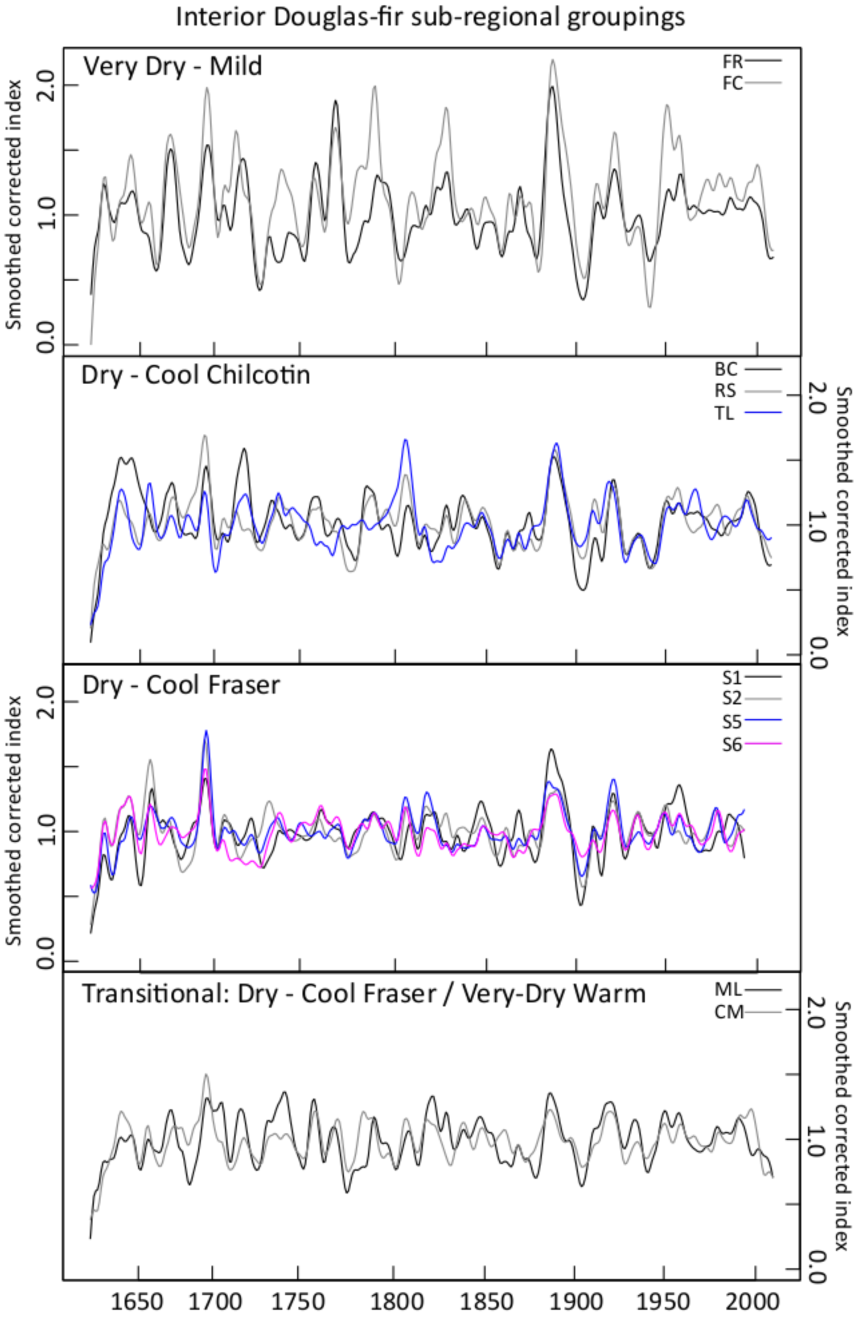

Figure 3.4 Smoothed (10-year spline) sub-regional chronologies plotted by biogeoclimatic unit. Start year truncated to 1632 and end year to 1994 for dry-cool Fraser sites and to 2009 for remaining sites (*see* Tables 3.1 and 3.2 for chronology abbreviations and biogeoclimatic unit descriptions).

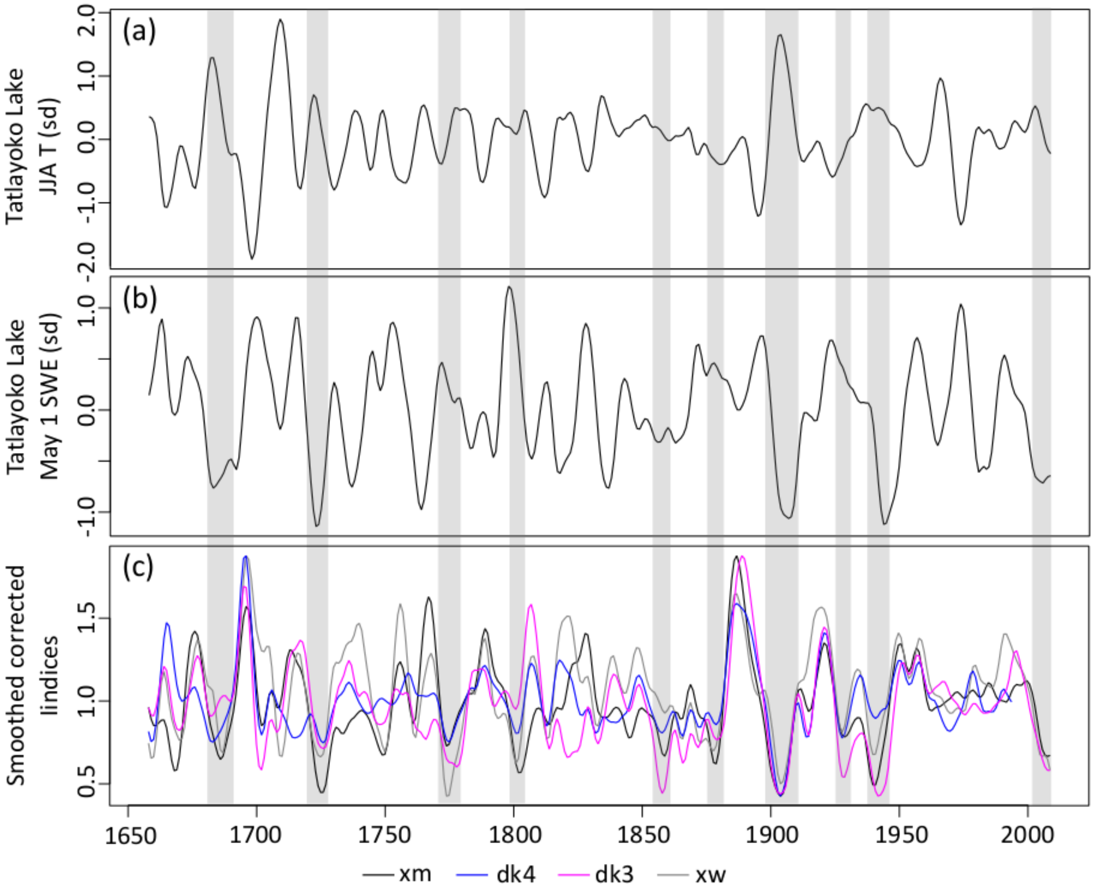

Figure 3.5 Relationship between reconstructed climatic variables (a & b; Starheim et al. 2013) and sub-regional western spruce budworm outbreak reconstructions (c) smoothed with a 10-year spline: (a) Tatlayoko Lake June-August temperature (JJA T) anomalies (sd=standard deviation); (b) Tatlayoko Lake May 1 snow water equivalence (SWE) anomalies; (c) sub-regional reconstructions (xm=very dry-mild, dk4=dry-cool Chilcotin, dk3=dry-cool Fraser, xw=very dry-warm). Grey shading corresponds to synchronous outbreak periods representing index values in the lowest 75% percentile for each sub-regional outbreak reconstruction.

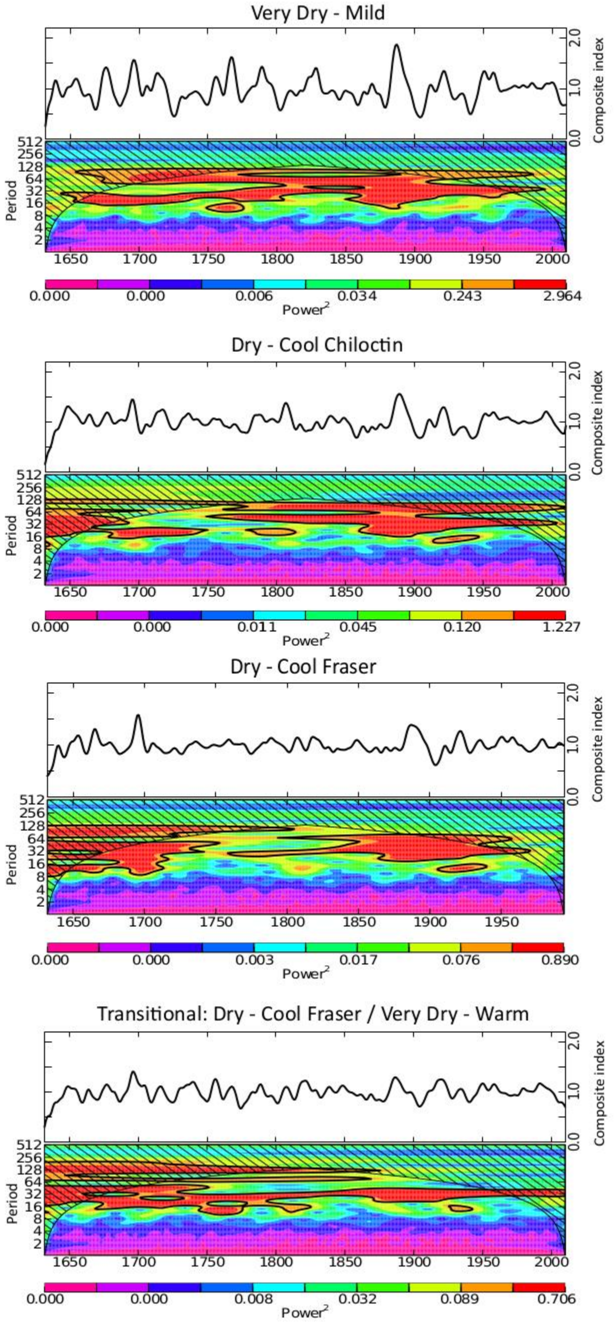

Figure 3.6 Sub-regional chronologies smoothed with a 10-year spine (top panel) and the wavelet power spectrum based on a continuous Morlet transformation (bottom panel). The cross-hatched region in lower panel of each plot is the cone of influence, where zero padding has reduced the variance, and the black contour encloses regions of greater than 99% confidence.

chronologies after the late 1700s and likely reflects more regular WSB outbreaks across the study area (Figs. 3.3 and 3.6). This low-frequency signal is the most prominent from the 1850s to present day. In the dry-cool Fraser sub-regional chronology, the wettest BEC unit in the study area (Table 3.2), and to some extent the transitional dry-cool Fraser to very-dry warm sub-regional chronology, there appears to be a quiescent phase in outbreak behavior from around 1725 to 1825 characterized by lower amplitude oscillations and lower power in the wavelet spectrum in the 32-year period (Fig. 3.6).

3.6 Discussion

Reconstruction of western spruce budworm dynamics in the Cariboo Forest Region indicates that outbreaks have been widespread and synchronous over the last four centuries. Over the period of record from 1576 to 2011 we identified 12 low-intensity outbreaks lasting on average 15 years with a return interval of 29.8 years (Table 3.5). This finding confirms that the outbreaks observed over the last 40 years in this region are not unprecedented and offers no support for the perception that the WSB has been expanding northward into the Cariboo Forest Region.

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

In this study we used two regional non-host controls and found that, for the common period, the reconstructed outbreaks had high fidelity in terms of timing, duration and frequency (Fig. 3.2). Sources of inconsistency between the two reconstructions were associated with the start and end years of outbreaks, a broad problem with the outbreak detection method employed here due to lag effects between budworm defoliation and subsequent growth suppression (Thomson and Van Sickle 1980, Alfaro et al. 1982, Swetnam and Lynch 1989) and in the intensity of individual outbreaks. For example, outbreak reconstructions using the regional lodgepole pine non-host show a higher intensity outbreak in the 1800s than the ponderosa pine non-host, while the reverse was true for the 1900s outbreak (Fig. 3.2b). We attribute these differences to the degree and type of climatic variability captured by each non-host (limitation 2 identified above), as well as the potential for local endogenous processes to be reflected in the year-to-year variation in the tree-ring series.

Using the longer regional ponderosa pine non-host chronology (Table 3.1), we identified 12 low-intensity WSB outbreaks over a 435-year period, or one outbreak approximately every 36 years. This finding is similar to those of Campbell et al. (2006) who identified 8 WSB outbreaks over a 300-year period or one outbreak approximately every 37 years in the southern interior of B.C. While we identified low-intensity events when ≥ 15% of trees recorded an outbreak, Campbell et al. (2006) identified an outbreak when ≥ 35% of trees recorded an outbreak (Table 3.5).

The application of a minimum threshold can be effective at differentiating between low and moderate intensity outbreaks. However, the threshold itself is somewhat subjective, as it is not based on theoretical or experimental values. It is possible that the threshold minimum of 35% may be too conservative and exclude small and/or low intensity events (Ann M. Lynch *personal communication*). Defoliation impacts are often highest among trees in the suppressed and intermediate height classes (Alfaro and Maclauchlan 1992), yet in our study (and others) canopy dominants were selected for reconstruction purposes to obtain the longest possible records. These individuals, however, may not be capturing the full impact of budworm feeding. When we increased the minimum threshold to 50% (moderate) the number of reconstructed outbreaks dropped to 5 (from 12) that on average lasted 11 years with a return interval of 64 years (Table 3.5). While the duration of low and moderate intensity events were similar (15 *versus* 11 years), the return interval increased two-fold (Table 3.5), which is consistent with return intervals reconstructed for WSB outbreaks in the Colorado Front Range (Ryerson et al. 2003).

Examining the corrected chronologies at the sub-regional scale provides another avenue to explore WSB outbreak dynamics across the study area, and illustrates the strong association between chronologies collected from the same BEC units (Fig. 3.4). The sub-regional chronologies highlight the strong fidelity between chronologies within group (i.e., BEC unit) and the synchronous WSB outbreak events across the study area, while also emphasizing the unique outbreak history at smaller spatial scales (Figs. 3.4 and 3.5). For example, chronologies in the very dry-mild BEC unit (FC and FR) are located on south facing slopes of the Fraser or Chilcotin Rivers and were characterized by a pronounced high amplitude signal when compared to the other sub-regional chronologies (Fig. 3.4). Chronologies from the dry-cool Fraser BEC unit (S1-S2, S5-S6) (Fig. 3.4), which is characterized by wetter and cooler conditions, have a notable quiescent phase from the early 1700s to the early 1800s (Figs. 3.4 and 3.5) that also corresponds to decreased power in the wavelet spectrum (Fig. 3.6). This suggests that site and/or stand conditions play an important role in mediating tree response to WSB outbreaks. For the very dry-mild sites conditions such as steep slopes, thin soils, and availability of soil moisture all likely contribute to increasing the sensitivity of these chronologies to negative (e.g., WSB defoliation) and positive (e.g., growing season moisture) stimulus. Conversely, the dry-cool Fraser sites, which were sampled at higher elevation (Table 3.1) and not from steep slopes, have a dampened sensitivity to environmental factors (Fig. 3.4). Site factors in combination with cooler and wetter climatic conditions (Table 3.2) are likely resulting in a more average growth response over time where tree grow is less responsive to events like budworm feeding (Fig. 3.4). The stand level to sub-regional scale WSB outbreak dynamics across the study area highlight the complex interactions between: site characteristics, canopy structure and composition, host plant quality, bud phenology, growth rates, tree resistance and climate, which to some extent all play a role in determining the intensity of individual outbreaks and tree growth responses across an area (Kozlowski 1969, Clancy 1992, Swetnam and Lynch 1993, Maclauchlan and Brooks 2009, Chen et al. 2003, Nealis 2012).

Synchronous outbreak periods in the Cariboo Forest Region in the 1720s, late 1700s, 1870s and 1930s (Fig. 3.5) were also present in the reconstructions from locations south of our study area (Campbell et al. 2005, 2006, Alfaro et al. 2008, 2014, Flower et al. 2014). Notably, the outbreak from 1898-1909 was a widespread event that appears in reconstructions in the area directly south of the Cariboo Forest Region (Campbell et al. 2006, Alfaro et al. 2014), the southern Okanagan (Alfaro et al. 2008, 2014), southern Vancouver Island (Harris et al. 1985), as well as in northeastern Oregon (Swetnam et al. 1995) and in stands found from central Oregon to western Montana (Flower et al. 2014). Three mechanisms have been suggested for coincident changes in the abundance of geographically discrete populations: dispersal of populations; dependence of population dynamics on a synchronous exogenous factor such as temperature or rainfall, essentially the “Moran” effect (Moran 1953); and, trophic interactions with populations of other species that are also spatially synchronous or mobile (Liebhold et al. 2004). Peltonen et al. (2002) studied spatial synchrony of forest insect outbreaks found that the Moran effect was likely the dominant mechanism causing spatial synchrony in outbreaks across regional scales and that dispersal was of lesser importance. This finding was supported by Swetnam and Lynch (1993) who also found that exogenous factors (e.g., climatic variability) played a significant role in regulating regional-scale WSB outbreaks in northern New Mexico. More recently, Flower et al. (2014) found that warm-dry climate preceded outbreaks by up to three years, but during outbreaks conditions tended to be cooler and wetter.

The comparison of regionally synchronous WSB outbreaks and climatic proxies from the western portion of the study area suggest that the influence of climate on outbreak dynamics is highly complex (Fig. 3.5). From the late 1600s to early 1700s and from the 1940s to the end of the record, synchronous outbreaks coincide with positive summer temperature and negative SWE anomalies indicative of warmer and drier climatic conditions (Fig. 3.5). However, from the late 1700s to the around the 1920s synchronous outbreaks coincide with negative temperature and positive SWE anomalies that are indicative of cooler and wetter climatic conditions (Fig. 3.5). During this same time period (with the exception of the 1920s) extensive wet periods prevailed across the southern Canadian Cordillera (Watson and Luckman 2004) and there were numerous episodes of glacial expansion in Mt. Waddington range west of the study area (Laroque and Smith 2003). During periods when warmer and drier conditions were associated with WSB outbreaks (Fig. 3.5), Starheim et al. (2013) found that the low-frequency signals associated ocean-atmospheric forcing, i.e., Pacific Decadal Oscillation and the Pacific North America Index were prominent in their hydroclimatic reconstructions.

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

In previous studies of WSB outbreak cycles, strong periodic components of ~30 and 40 years over centuries have been documented using Single Spectrum Analysis (Ryerson et al. 2003, Campbell et al. 2006, Alfaro et al. 2014), and are similar to periods found by Swetnam and Lynch (1993). In eastern Canada, eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) populations have oscillated more or less periodically over two centuries with an average period of 35 years (Royama 1984). In this study, a continuous Morlet wavelet transform of the sub-regional chronologies revealed strong modes of variability ranging from 16 to 64-year cycles (Fig. 3.6), which is consistent with other studies. The beginning of the outbreak chronologies, early 1600s to mid-1700s, was characterized by the high frequency 16-year pattern suggesting that WSB outbreak occurred with greater frequency during the 15-16th centuries (Fig. 3.6). The lower-frequency 32-year period became more evident after the late 1700s, which is coherent with the analysis of the return intervals of WSB outbreaks (Table 3.5) and coincides to the period when cooler and wetter conditions were associated with regionally synchronous WSB outbreaks (Figs. 3.5 and 3.6). In all of the sub-regional chronologies this low-frequency 32-year period became prominent after the mid-1850s suggesting that WSB outbreaks became more temporally stable after this time (Fig. 3.6). Widespread outbreaks across the study area (Fig. 3.5), and outbreak periodicities with an average of 32-years (Fig. 3.6) supports previous research that climate may have a synchronizing influence on outbreak dynamics at larger spatial scales (Royama 1984, Williams and Liebhold 2000, Peltonen et al. 2002, Jardon et al. 2003). However, more detailed analysis of a variety of climatic parameters is required to corroborate this in our study area.

3.7 Conclusion

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

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

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

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Chapter 4 Variation in wood anatomical structure of Douglas-fir defoliated by the western spruce budworm: A case study in the coastal-transitional zone of British Columbia, Canada

4.1 Article information

This chapter consists of an article published in the journal Trees.

4.1.1 Authors' names and affiliations

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4.1.2 Authors' contributions

J.A. developed the study and hypothesis, conducted field, laboratory work, and statistical testing, wrote the manuscript and produced all tables and figures. A.B.

supported statistical analyses. R.A. assisted in re-locating original permanent sample plots, provided the permanent plot dataset, contributed editorial support to Study Area and Methods sections, and reviewed and edited the manuscript. D.S. assisted in hypothesis development, contributed to the Introduction, Methods and Results sections and reviewed and edited the manuscript. H.G. contributed to hypothesis development, methodological development, supported wood anatomy and micro sectioning methods and interpretation, and reviewed and edited the manuscript.

4.1.3 Citation

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4.2 Abstract

Western spruce budworm (*Choristoneura occidentalis* Freeman) is a widespread and destructive defoliator of commercially important coniferous forests in western North America. In British Columbia, Canada, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the most important and widely distributed host. Permanent sample plots were established at a number of locations in southern interior at the beginning of a severe western spruce budworm outbreak in the 1970s. Two of the sites were sampled in 2012 to determine whether modifications had occurred in the anatomical characteristics of stem wood formed during outbreak years. We determined that rings formed during the western spruce budworm 1976-1980 outbreak had a significantly lower percent latewood, reduced cell wall thickness and smaller radial cell diameters. While the cellular characteristics of the earlywood remained fairly constant, significant reductions in lumen area occurred in 1978 and 1979 at each site. Our study shows that western spruce budworm outbreaks not only reduce annual radial growth, but also temporarily modify cellular characteristics in latewood cells, which has implications for wood density and quality in Douglas-fir.

Keywords: Cellular anatomy; tracheids; dendroecology; Douglas-fir; western spruce budworm; defoliation event

4.3 Introduction

Western spruce budworm (*Choristoneura occidentalis* Freeman; WSB) is the most widespread and destructive defoliator of coniferous forests in western North America (Wickman et al. 1992, Mason et al. 1997). Populations of WSB periodically intensify due to increased reproduction and survival, resulting in outbreaks that typically last for several years over large geographical areas (Alfaro et al. 2014). WSB defoliation severely reduces the radial growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) host-trees (Furniss and Carolin 1977, Fellin and Dewey 1982), with sustained outbreaks resulting in stem defects, mortality in understory trees, and regeneration delays due to feeding of staminate flowers and developing cones (Alfaro et al. 1982, Fellin and Dewey 1982, Alfaro and Maclauchlan 1992, Maclauchlan et al. 2006).

In the last two decades WSB outbreaks within the Douglas-fir forests of the interior of British Columbia (B.C.), Canada, have increased in severity, frequency and spatial distribution (Maclauchlan et al. 2006) in response to ongoing climate change (Dale et al. 2001, Logan et al. 2003, Volney and Hirsch 2005, Battisti 2008). Given that Douglas-fir is a widely distributed and commercially important species in this region, its increased vulnerability to WSB outbreaks (Walker and Sydenysmith 2008) is having immediate economic and social consequences for forestry dependent communities (Spittlehouse 2008, Johnston et al. 2010). These issues are excaberated by the recent catastrophic outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in this region that resulted in the cumulative mortality of over 710 million m^3 of *Pinus* trees (BCMOFLNRO 2012). Given the long-term loss of this timber resource, forest managers have refocused their attention on minimizing the impact of WSB outbreaks on Douglas-fir forests through application of the biological agent *Bacillus thuringiensis* var. *kurstaki*

(Buxton and Maclauchlan 2001-2012). While the expectation is that a reduction in the incidence of outbreaks would enhance wood formation by minimizing growth suppression, stem defects and mortality, there has been an absence of anatomical research focused on evaluating the cellular-level impact of WSB on Douglas-fir growth. Given the increasing importance of Douglas-fir to the forest industry, and the uncertain impact of climate change on disturbances arising from WSB outbreaks, it is crucial to aquire a fundamental understanding of the cellular-level changes in anatomical structure resulting from defoliation during WSB outbreaks.

The goal of this study was to evaluate the anatomical characteristics of Douglas-fir trees impacted during an outbreak of the WSB by examing inter-annual changes in xylem characteristics in stem wood formed during an outbreak, relative to wood formed during non-outbreak years. The findings of the research will contribute to our understanding of the effects of WSB defoliation on wood density, wood quality properties, and the resilience and plasticity of Douglas-fir.

4.3.1 Study sites

In the 1970s a number of permanent sample plots (PSPs) were established in southwestern B.C. during a WSB outbreak to study the effects of defoliation on stand structure, tree growth, volume, and tree form. Two PSPs located in the Fraser River Canyon, approximately 200 km northeast of Vancouver, B.C., were selected for this study: East Anderson (49°46’34” N, 121°21’05” W) and Gilt Creek (49°42’05” N, 121°22’35” W). Both PSPs are located on steep slopes (25° and 34°, respectively) between 660 and 700 m asl and have similar south-facing aspects (Fig. 4.1).

The two PSPs are found in a region that is climatically transitional between the B.C. coast and the interior characterized by warm-dry summers and moist-cool winters with moderate snowfall (Green and Klinka 1994). Interpolated climate data (ClimateBC, v4.71; Wang et al. 2006, 2012) indicate the mean annual temperature is 6.3° C, with spring and summer temperatures averaging 12°C and 23°C, respectively. Annual precipitation totals in this setting average 1587 mm, 72% of which falls in the autumn and winter seasons. Dry summers in the study area historically gave rise to stand replacing fires, resulting in even-aged Douglas-fir forests with minor components of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red cedar (*Thuja plicata* Donn ex D. Don). Both PSPs are characterized by poorly developed shrub and herb layers in the understory, but have a well-developed moss layer, dominated by step moss (*Hylocomium splendens* (Hedw.) Br. et Sch.), and red-stemmed feather moss (*Pleurozium schreberi* (Brid.) Mitt.) (Green and Klinka 1994).

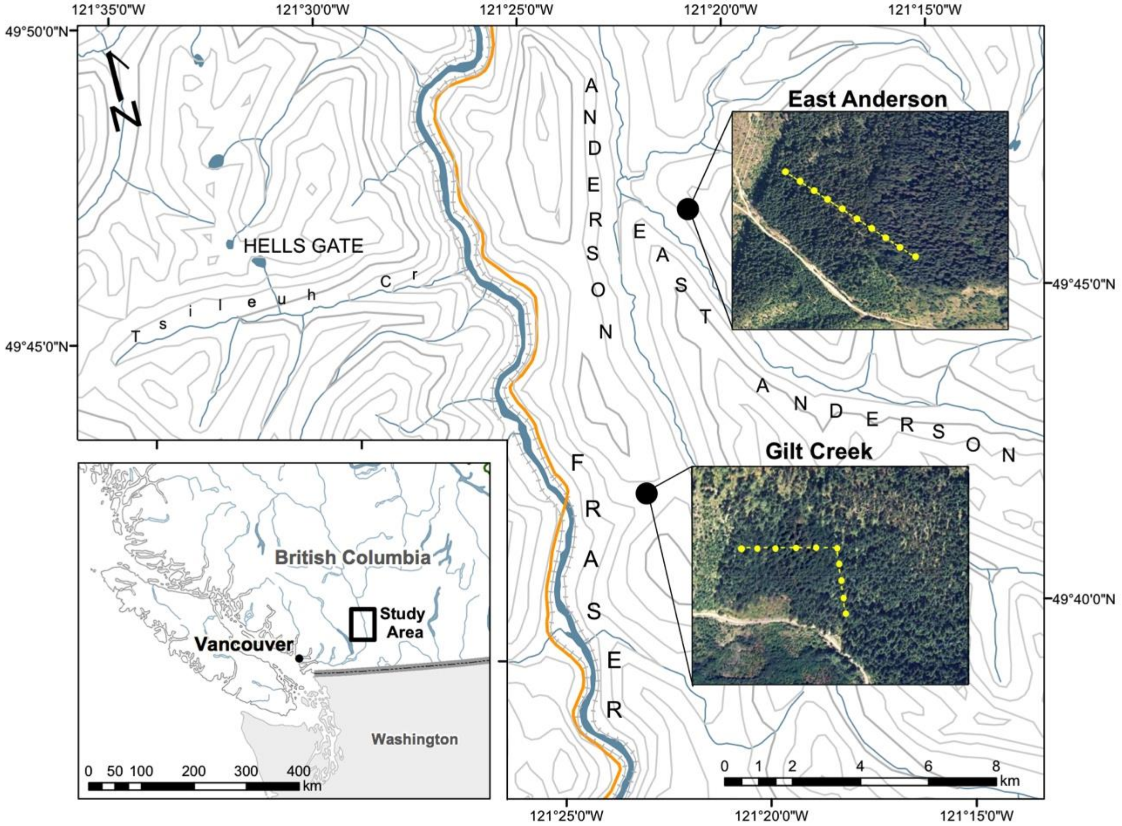

Figure 4.1 Location of 2 permanent sample plots, East Anderson and Gilt Creek, used to measure impacts of western spruce budworm on cellular anatomy of stem wood in Douglas-fir British Columbia, Canada. Inset maps of 2003 orthophoto images showing the single plots (white dots) with an inter-plot spacing of 80 metres.

The East Anderson and Gilt Creek PSPs were established in 1976, at the beginning of a WSB outbreak that lasted from 1976 to 1980. At both sites the original sampling strategy was designed to incorporate 10 plots that transected the forest type (i.e., forest polygon with homogenous structure and composition) with inter-plot spacing of 80 m (Fig. 4.1). Initial stand structure was determined using a variable radius prism with a basal area factor of 5 (m^2/hectare). Each plot tree was measured for diameter at breast height (cm), total tree height (m), and stem features such as topkill (i.e., dieback of the apical portion of the tree top due to severe defoliation). Annual visual defoliation data was collected from 1976 to 1980 at East Anderson and from 1977 to 1979 at Gilt Creek from the top, middle and bottom thirds of the crown. In 1982 these parameters were re-measured, by which time the WSB outbreak had collapsed and defoliation levels were zero.

4.4 Methodology

4.4.1 Field procedures

The East Anderson and Gilt Creek PSPs were revisited in August 2012, 36 years after their establishment. To study the effect of defoliation on tree growth, two 5.2 mm increment cores were collected from 25 trees in each PSP at ground and breast height, 0.3 m and 1.3 m respectively. To study the effects of defoliation on wood anatomy, a single 12 mm core was collected at breast height core from the same trees.

4.4.2 Laboratory

Tree-ring chronologies were developed using standard dendrochronological methodologies (Stokes and Smiley 1968). Polished tree rings were measured with WinDendro (Ver. 2009d, Regents Instruments Inc. 2009) at a precision of 0.01 mm, and subsequently visually crossdated and verified using COFECHA (Holmes 1986) to ensure exact calendar years were assigned to each tree ring. Individual tree-ring series were standardized using a negative exponential curve to remove biological growth trends (Cook et al. 2007), and stand-level chronologies were developed by computed a bi-weight robust mean that minimizes the effect of outliers and produces a dimensionless stationary index with a defined mean of 1.0 (Cook and Kairiukstis 1990).

For anatomical measurements, the 12 mm cores were cut into 4 to 5 cm segments and the portion spanning the years 1973 to 1988 identified for further analysis. Core segments were split radially and micro sections were cut on the cross-sectional plane using a GSL1 microtome (Gärtner et al. 2014) equipped with removable NT-cutter blades. Micro sections were cut to a thickness of 15 µm using a non-Newtonian fluid (Schneider and Gärtner 2013), which greatly reduced preparation problems related to the separation of secondary cell walls and cell distortion, especially in the earlywood portion of the rings. Micro sections were double stained with cellulose and lignin specific dyes (Astrablue and Safranin), dehydrated with alcohol, rinsed in Xylol and embedded in Canada balsam (Gärtner and Schweingruber 2013). Permanent slides were photographed with a digital camera system (Colorview IIIu camera mounted on an Olympus BX41 microscope) at 40x magnification.

4.4.3 Analysis

Twenty micro sections were measured (e.g., Fig. A1) using WinCell (Ver. 2004a, Regents Instruments Inc. 2004). Twelve annual rings were measured (1974 to 1986) along 10-14 radial files per ring on each sample, with the following parameters recorded: percentage latewood (%), cell lumen area (µm^2), cell wall thickness (µm), and radial cell diameter (µm). Every cell along each radial file was measured, and cellular parameters were averaged into a single radial file value for earlywood and latewood.

All statistical analyses were performed using the software R, version 3.0.2 (R Core Team 2013). The non-parametric Kruskal-Wallis (Quinn and Keough 2002) was computed to test for differences in wood anatomical properties between individual defoliated years (1976 to 1980), post-defoliation years (1981 to 1983) and non-defoliated periods 1974-1975 and 1984-1986 ($p < 0.05$). After a significant Kruskal-Wallis test result, the multiple comparison test *kruskalmc* from the R library *pgirmess* was applied to determine which groups were different from one another (Giraudoux 2013). Individual years had to be significantly different from both non-defoliated periods to reject the null hypothesis, and only differences between individual years and the non-defoliated periods were evaluated. Details of the Kruskal-Wallis test and the outcome of multiple comparisons were summarized by the anatomical parameter tested: percentage of latewood tracheids (%); lumen area (μm^2); secondary cell wall thickness (μm); and, radial cell diameter (μm). We averaged annual radial file data into a single ring value for each year and each micro section to assist in visual interpretation. For visualization, a smoothing spline using a locally weighted regression was added to scatterplots of anatomical variables to highlight the trends, and the standard error of the smoothed surface (Wickham and Chang 2013).

4.5 Results

4.5.1 Defoliation history

Defoliation at East Anderson in 1976 averaged 50% of the crown area (no data for Gilt Creek), and peaked at both sites in 1977, when an average 65% (East Anderson) and 60% (Gilt Creek) of the crowns were defoliated. After 1977, average defoliation decreased at East Anderson to 60% (1978), 40% (1979) and 20% (1980), while at Gilt Creek average defoliation stayed relatively constant at 55% in 1978 and 1979 (no data for 1980) (Fig. 4.2).

4.5.2 Dendrochronology

The tree ring data indicates that tree establishment occurred in the early 1900s at East Anderson and in the 1890s at Gilt Creek (Table 4.1; Fig. 4.3). The standard deviation around establishment dates was greater for Gilt Creek indicating that the age structure was more variable at this site (Table 4.1). Tree-ring series at each site strongly crossdate, as indicated by the inter-series *r* statistic that was well above the value of 0.328 ($p<0.01$) (Table 4.1). Standardized tree-ring indices, truncated to the average

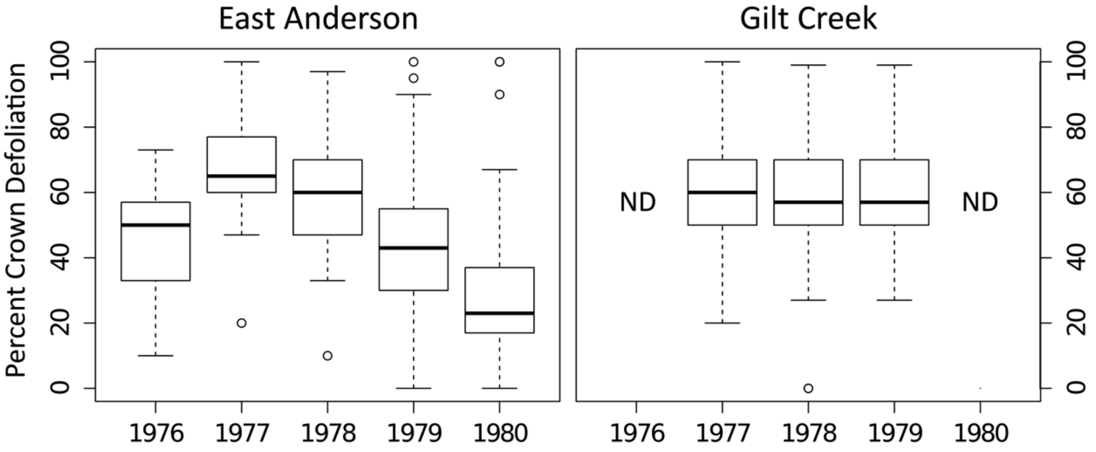

Figure 4.2 Average crown defoliation (%) (ND = no data) during the 1970s outbreak at East Anderson and Gilt Creek permanent sample plots. Boxes represent the interquartile range and median, whiskers indicate the variability outside the upper and lower quartiles, and outliers are plotted as individual points.

establishment year, show inter-annual variability around the reference mean of 1.0 at both PSPs (Fig. 4.3a). The 1970s outbreak is evident in the tree ring series as a pronounced period of growth suppression starting in 1976 and ending in 1983 (Fig. 4.3a), a duration that corresponds to the typical tree ring signature of WSB outbreaks (Alfaro et al. 1982).

Table 4.1 Properties of tree ring data from permanent sample plots used to measure impacts of western spruce budworm on wood cell anatomy of Douglas-fir, British Columbia, Canada.

Stand Name	Length of master tree ring series	Mean year of tree establishment* (±SD)	Inter-series *r*	Number of dated series
East Anderson	1892-2011	1904 (±15)	0.57	47
Gilt Creek	1800-2011	1890 (±43)	0.59	38

* Mean year of establishment based on crossdated cores collected at stump height (0.3m) with standard deviation in brackets.

Individual (i.e., non-averaged) raw ring growth (mm) increment value for the analysis window 1974 to 1986 demonstrated high inter-tree variability in growth during the 1970s outbreak at East Anderson (Fig. 4.3b) and Gilt Creek (Fig. 4.3c), as well as the strong growth suppression in response to budworm feeding. Annual growth rates at East Anderson were 1.2 mm pre- and post-outbreak, decreasing to a low of 0.2 mm during defoliation years (Fig. 4.3b). At Gilt Creek pre- and post-outbreak growth rates were slightly lower at 1.0 mm, and decreased to around 0.1 mm during the defoliation period

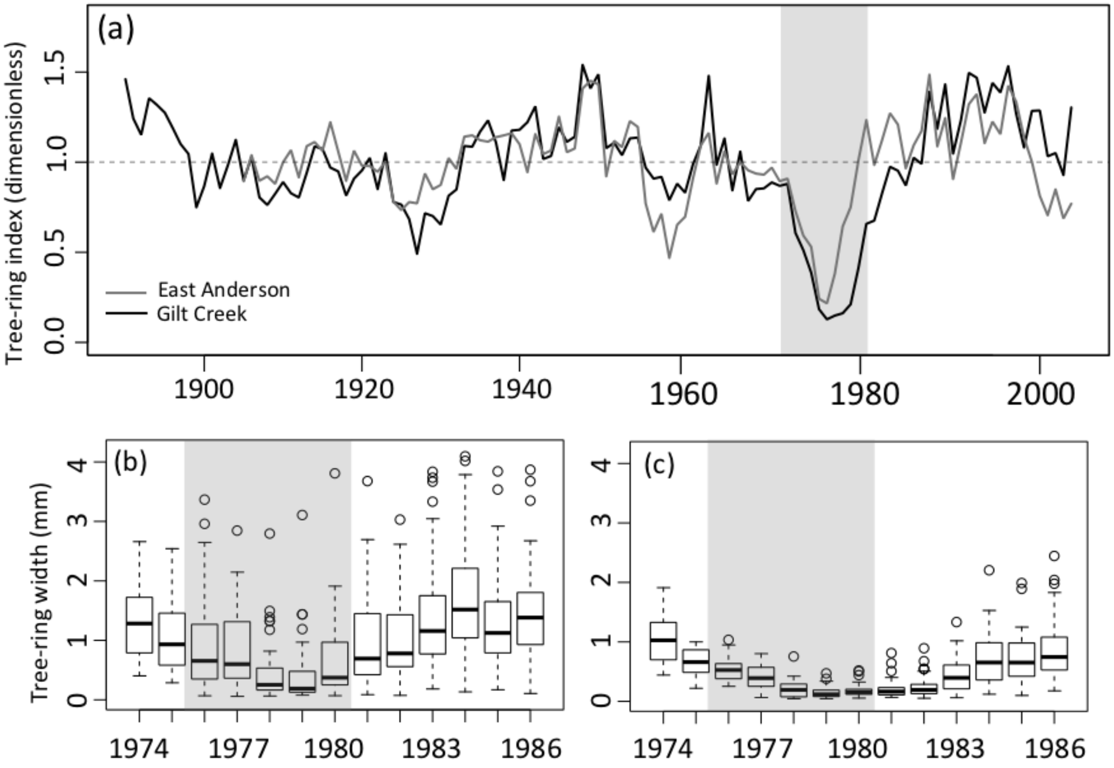

Figure 4.3 a) Tree ring index series truncated to average year of tree establishment, dashed line indicated chronology mean (1.0); b) East Anderson raw tree ring growth (mm) during analysis window, 1974-1986; c) Gilt Creek raw tree ring growth (mm) during analysis window, 1974-1986. Boxes represent the interquartile range and median, whiskers indicate the variability outside the upper and lower quartiles, and outliers are plotted as individual points. Gray shading highlights the western spruce budworm outbreak period from 1976 to 1980.

(Fig. 4.3c). At both PSPs the lowest growth increment occurred in 1979, two years after the maximum crown defoliation in 1977 (Fig. 4.2 and 4.3). Annual growth increment and inter-tree variability, as evidenced by outliers, was higher at East Anderson than at Gilt Creek (Fig. 4.3b and 4.3c).

4.5.3 Wood anatomy

Twenty high quality micro sections were measured over a 12-year period from 1974 to 1986 from each PSP (e.g., Figs. 4.4, A2 to A3). See Appendix I for summary statistics averaged by year (Tables A1 to A6). Table 4.2 summarizes the Kruskal-Wallis test and multiple comparisons for each anatomical parameter tested. The percent latewood decreased in both PSPs during the outbreak period (Fig. 4.5); at East Anderson this effect lasted from 1977 to 1979 with a 20% reduction in the percent latewood (Table 4.2). At Gilt Creek there was a 13% reduction in latewood in 1979 and 1981 (Table 4.2). For the other cellular parameters three main trends were evident: a) independent of the parameter analyzed reductions in area or size were observed during defoliation years as compared to the years with no defoliation; b) reductions in cell wall thickness and radial cell diameter in the latewood tracheids were the most acute and prolonged of any of the parameters analyzed; and, c) the largest reductions occurred in 1979 (Fig. 4.5).

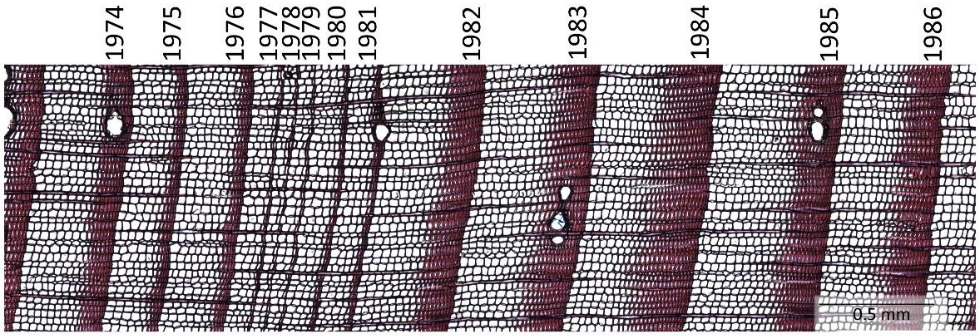

Figure 4.4 Example of a composite micro section for analysis window (1974 to 1986) at East Anderson permanent sample plot.

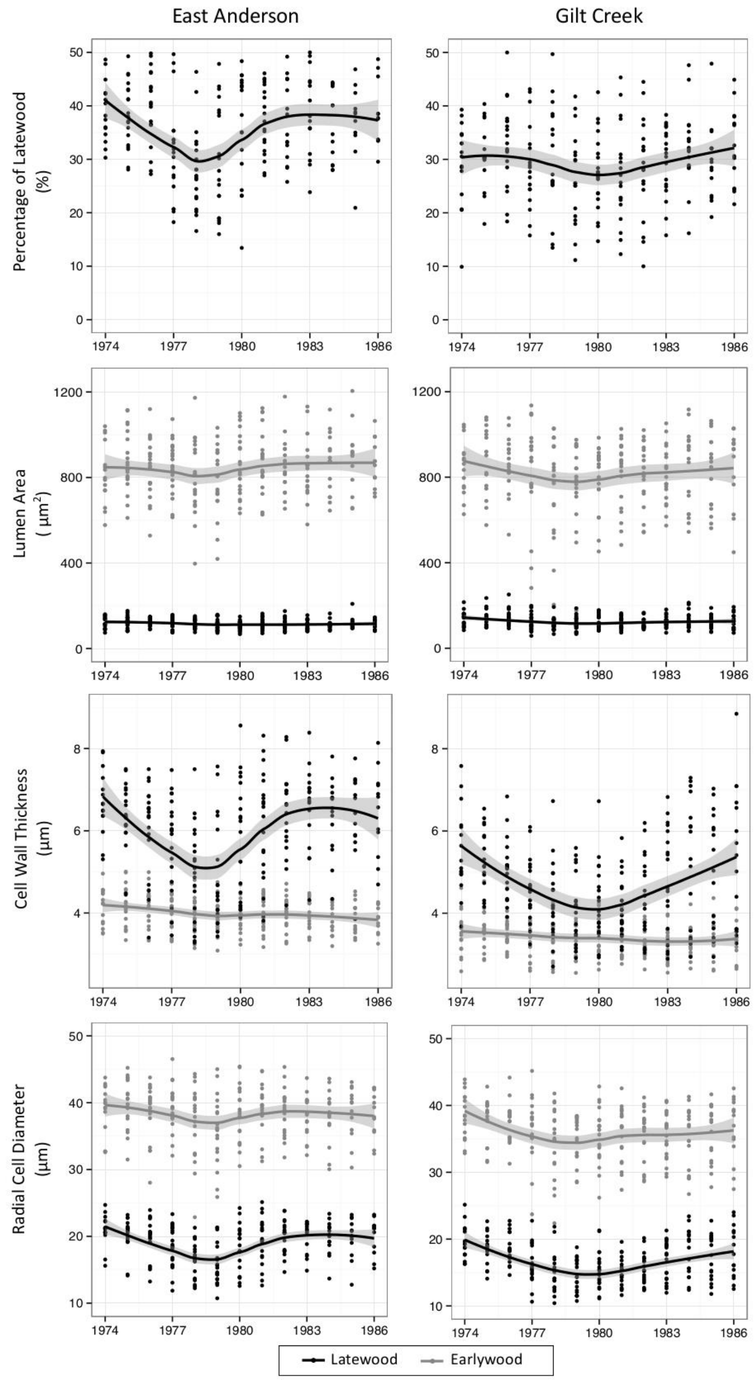

Figure 4.5 Scatterplots (fit with a locally weighed regression line) of anatomical parameters: percent latewood (top), lumen area (top-middle), cell-wall-thickness (bottom-middle), and radial cell diameter (bottom) for earlywood (grey) and latewood tracheids (black) at East Anderson (left) and Gilt Creek (right) permanent sample plots.

Table 4.2 Kruskal-Wallis test for each anatomical parameter: percent latewood, lumen area, cell wall thickness, and radial cell diameter for early- and latewood tracheids. Multiple comparisons determined where significant differences occurred between tracheids produced during defoliation years and undefoliated years (1974-75 and 1984-86). Significant differences are denoted by * at the $p<0.5$ level and ** at the $p<0.01$ level. Individual outbreak or post-outbreak years had to be significantly different from both sets of undefoliated years to reject the null hypothesis, and differences between individual years were not considered at permanent sample plots East Anderson and Gilt Creek.

			Difference between year and undefoliated periods (1974-75 & 1984-86)							
Tracheid Type	Cell Parameter	Kruskal-Wallis p-value	1976	1977	1978	1979	1980	1981	1982	1983
East Anderson										
Earlywood	Lumen Area (μm^2)	$p = 3.6^{-06}$			*	**				
	Cell Wall Thickness (µm)	$p < 0.001$								
	Radial Cell Diameter (µm)	$p < 0.001$			*	**				
Latewood	Percent Latewood (%)	$p < 0.001$		**	**	**				
	Lumen Area (μm^2)	$p = 1.1^{-09}$								
	Cell Wall Thickness (µm)	$p < 0.001$		**	**	**	**			
	Radial Cell Diameter (µm)	$p < 0.001$		**	**	**	**			
Gilt Creek										
Earlywood	Lumen Area (μm^2)	$p = 4.6^{-07}$			**	*				
	Cell Wall Thickness (µm)	$p = 5.3^{-13}$								
	Radial Cell Diameter (µm)	$p < 0.001$								
Latewood	Percent Latewood (%)	$p < 0.001$				**		**		
	Lumen Area (μm^2)	$p < 0.001$			*	*				
	Cell Wall Thickness (µm)	$p < 0.001$			**	**	**	**	**	
	Radial Cell Diameter (µm)	$p < 0.001$		**	**	**	**	**	**	

At East Anderson earlywood lumen area and radial cell diameter decreased between 5% to 8% in 1978 and 1979 compared to undefoliated years; in the latewood tracheids cell well thickness decreased between 11% to 25% from 1977 to 1980, and radial cell diameter decreased between 8% to 22% from 1977 to 1980 compared to undefoliated years (Fig. 4.5). At Gilt Creek earlywood lumen area decreased by 10% and 12% in 1978 and 1979 respectively, compared to undefoliated years (Table 4.2); in the latewood tracheids lumen area decreased by 13% in 1978 and 1979, cell wall thickness decreased between 18% and 22% from 1977 to 1982, and radial cell diameter was 12% to 22% smaller from 1977 to 1982 compared undefoliated years (Fig. 4.5).

4.6 Discussion

We examined cellular variations in the wood anatomy of Douglas-fir trees arising from severe WSB defoliation at two sites during the late 1970s. We are unaware of other studies that have examined the anatomical characteristics of Douglas-fir in relation to defoliation by the WSB, either in artificial defoliation experiments or naturally occurring outbreaks in mature forest stands. We hypothesized that in addition to radial growth suppression (Kulman1971, Alfaro et al. 1982) that anatomical parameters such as percent latewood, lumen area, cell wall thickness, and/or radial cell diameter would change in the stem wood during an outbreak of the WSB.

In this study, reductions in radial increment during the defoliation period were 80% at East Anderson and 83% at Gilt Creek (Fig. 4.3), corresponding to an average of 60% defoliation of the crown (Fig. 4.2). Growth suppression was immediate at each site (Fig. 4.3) and persisted for approximately 8 years. Radial growth has been shown to be progressively reduced with every consecutive year of defoliation, in a cause-effect relationship that usually has a 1- to 2-year lag (Alfaro et al. 1982). This lag was apparent in the patterns of radial tree-growth at both sites (Fig. 4.3), where the maximum growth reduction (1979) did not occur until 2 years after maximum crown defoliation (1977). This 2-year lag was also evident in the anatomical variables tested.

Significant inter-annual changes in xylem characteristics, principally in latewood tracheids, were detected. When compared to non-outbreak years these changes include decreases in percent latewood, cell wall thickness and radial cell diameter during WSB defoliation (Table 4.2; Fig. 4.5). In contrast, very few sustained changes were detected in earlywood tracheids (Table 4.2; Fig. 4.5). The percentage of latewood in growth rings is the main driver of overall wood density (Zobel and Van Buijtenen 1989), which from a timber perspective is the most important feature of Douglas-fir (Renninger et al. 2006). In Douglas-fir, percent latewood has been shown to decrease after thinning and fertilization treatments (Brix and Mitchell 1980) and exposure to air pollution (de Kort et al. 1991, de Kort 1993). In slow growing Douglas-fir infected with Swiss needle cast (*Phaeocryptopus gaeumannii* (Rohde) Petrak), a disease that reduces the leaf area of infected individuals, trees produced higher percent latewood and had better strength characteristics (Johnson et al. 2003). In this study we found that during WSB defoliation percent latewood was significantly lower at both sites (Table 4.2; Fig. 4.5) suggesting that slower radial growth did not necessarily lead to denser wood. However, the degree of latewood reduction required to meaningfully impact wood density is unclear and was not one of the goals of this study.

We suggest that the changes in latewood tracheid properties identified in this study are related to the timing of latewood formation, as well as processes such as cell wall thickening, and budworm phenology and feeding behavior. In Douglas-fir, vegetative bud burst occurs in mid-May (Owens 1968) but can occur as early as mid-April in coastal regions (Brix and Mitchell 1980). Early-stage WSB larvae emerge several days to weeks in advance of bud suitability (i.e., bud burst) (Nealis 2012) and then feed on buds and new needles until early-July, after which they pupate (Furniss and Carolin 1977). By this time earlywood formation is complete and latewood transition and formation is underway (Brix and Mitchell 1980, Li and Adams 1994, Vargas-Hernandez and Adams 1994, Johnson et al. 2005). Consequently latewood formation, including cell wall thickening, occurs when the tree has undergone its maximum defoliation in a given year and foliar resources are the lowest.

The extent to which tree growth, and by association cellular properties, are a function of carbon availability has important implications for the understanding and predicting tree and forest responses to environmental change (Sala et al. 2012). The removal of current-year shoots near the beginning of the growth period stimulates starch mobilization to increase net photosynthetic rate of the remaining foliage (Reich et al. 1993, Lavigne et al. 2001). In artificially defoliated young red pine (*Pinus resinosa* Ait.) photosynthetic rate and leaf conductance increased due to altered root: needle balance, leading to a shift in allocation to new needles rather than the roots, followed by a temporary increase in photosynthesis. This compensatory response has a net energy cost and carbohydrate reserves were lower in defoliated individuals (Reich et al. 1993). Foliage replacement requires carbon reserves for the production of new needles at a considerable energy cost for tree, and cumulative loss of current-year foliage results in gradually consumed and depleted carbohydrate reserves (Reich et al. 1993). In Douglas-fir stands infected with Swiss needle cast, retention of non-structural carbohydrates in the crown has a greater priority than exporting photosynthates required for diameter growth in the trunk ensuring crown growth was favoured (Saffell et al. 2014). Plants allocate carbohydrates to different sinks, and foliage production takes priority over stem growth to ensure that there is an adequate amount of resources available for developing foliage (Piene and Little 1990, Kaitaniemi et al. 1999, Polák et al. 2006). Thus, carbon storage may be an active sink, where trees actively regulate storage at the expense of short-term growth to optimize growth and survival in the long-term (Sala et al. 2012).

While the growth response of latewood tracheids was similar at each site (Table 4.2; Fig. 4.5), they were most pronounced and prolonged at Gilt Creek where the defoliation pressures were highest. Crown defoliation at Gilt Creek averaged 60% from 1977 to 1979 (Fig. 4.2). More intense budworm feeding extended the lag effect at Gilt Creek, where the growth suppression phase (Fig. 4.3) and reductions in cell wall thickness and radial cell diameter (Fig. 4.5) persisted through the outbreak phase and into non-outbreak years (1981 through 1982) (Table 4.2). This prolonged response was not evident at East Anderson where defoliation levels steadily decreased after 1977 to around

20% by 1980 (Fig. 4.2), suggesting that defoliation intensity is a particularly important feature to consider when evaluating tree response to herbivory (Kozlowski 1969, Kulman 1971, Alfaro et al. 1985, Krause and Raffa 1996). The modifications to latewood tracheid properties during a WSB outbreak, especially when prolonged, may impact the drought tolerance of Douglas-fir as latewood has been shown to have a greater water storage capacity then earlywood (Domec and Gartner 2002). Thus trees with higher wood density with thicker cell walls and smaller lumen diameters are expected to be more resistant to drought (Martinez-Meier et al. 2008, Dalla-Salda et al. 2009).

Rossi et al. (2009) conducted a study where spruce budworm (*Choristoneura fumiferana* Clemens) defoliation was simulated by removing two-thirds of the current-year needles in balsam fir (*Abies balsamea* (L.) Mill.) seedlings. This removal had no effect on either cambial activity or xylem differentiation in the stem, or the anatomy of the xylem produced. Significant changes in xylem anatomy in the stem wood (Filion and Cournoyer 1995, Liang et al. 1997) was, however, detected during the study of a mature eastern larch (*Larix laricina* (Du Roi) K. Koch) forest in subarctic Quebec during a larch sawfly (*Pristiphora ericsonii* (Htg.)) defoliation event. Filion and Cournoyer (1995) found that a light ring formed in the first year of the outbreak, and in subsequent years the tracheid size decreased abruptly in the most severely impacted trees. Liang et al. (1997) compared light rings resulting from sawfly defoliation and climate-limiting conditions. They demonstrated that average latewood cell wall thickness was reduced in insect-generated light rings, and smaller still in climate-induced light rings, while cell wall thickness in earlywood tracheids remained constant.

In natural outbreak conditions insect defoliation varies in intensity according both to the severity of the attack and to the vigour of the tree at the time, consequently tree response to defoliation is highly variable and light rings due to defoliation are more variable than those produced by climatic conditions (Liang et al. 1997). In experimental conditions trees (seedlings or juveniles) are growing in controlled environments and receiving the same defoliation treatments (Wodzicki 2001, Rossi et al. 2009). However, mature trees undergoing natural defoliation sustain different feeding pressures, and have different physiological status, and vigour. The complexity of host plant reaction to insect defoliation can be important in contributing to the variability of cell structure patterns among different years and different trees (Liang et al. 1997). This pattern was readily apparent in this study where cell structure patterns were highly variable between earlywood and latewood tracheids, and between non-outbreak and outbreak years from tree to tree (Fig. 4.5).

4.7 Conclusions

In this study we focused attention on the anatomical impact of a single WSB outbreak in Douglas-fir stem wood collected at breast height. We demonstrated that this outbreak resulted in statistically significant annual reductions in the percentage of latewood, cell wall thickness and radial cell diameter. As environmental factors affect whole plants not just stem wood (Gartner et al. 2002), future research should examine the anatomical impact of multiple WSB outbreaks in samples collected at different heights on the tree bole, branches and roots. This approach would provide additional insight into the cumulative effects of outbreak disturbances on wood structure and would enhance our understanding of how different parts of a tree respond to these disturbances. Further, sampling on the tangential plane could provide insights into the response of other anatomical structures, such as ray parenchyma cells in nutrient storage during disturbances events.

4.8 Acknowledgements

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Chapter 5 Variations in wood anatomical structure of interior Douglas-fir defoliated by the western spruce budworm: A case study in the xeric zone of southern British Columbia, Canada

5.1 Article information

Chapter 5 consists of an unpublished manuscript that will be prepared for publication in a peer-reviewed journal.

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5.1.2 Authors' contributions

J.A. developed the study and hypothesis, conducted field, laboratory work, and statistical testing, wrote the manuscript and produced all tables and figures. R.A. assisted in hypothesis development, and reviewed and edited the manuscript. D.S. assisted in hypothesis development, and reviewed and edited the manuscript. H.G. contributed to hypothesis development, methodological development, supported wood anatomy and micro sectioning methods and interpretation, and reviewed and edited the manuscript.

5.2 Abstract

Western spruce budworm (*Choristoneura occidentalis* Freeman) is a widespread and destructive defoliator of commercially important Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) forests in the interior of British Columbia. In 2012, Douglas-fir samples were taken from two sites, were micro sectioned and examined to determine how climatic variability, stand competition and western spruce budworm damage affected stemwood anatomical characteristics. Study sites, located in the xeric southern interior, had been monitored annually for western spruce budworm defoliation over a prolonged outbreak from 1997 through 2012. We determined that xylem formed during the western spruce budworm outbreak had progressively larger earlywood lumen area and radial cell diameter, reduced mean latewood cell wall thickness and smaller radial cell diameters, and decreased percent latewood. Mixed effects models indicated that maximum spring temperature and spring precipitation (Site 3) and canopy class and defoliation severity (Site 4) were the best predictors for earlywood tracheids. For latewood tracheids, cell wall thickness and radial cell diameters were best predicted by spring precipitation, June precipitation, and cumulative defoliation (Site 3); and by June precipitation and maximum spring temperature (Site 4). Percentage of latewood was best predicted by June precipitation and July precipitation (Site 3), and by maximum spring temperature and spring precipitation (Site 4). Western spruce budworm defoliation reduces annual radial growth, and affects micro anatomical characteristics in earlywood and latewood tracheids. Defoliation severity and duration, as well as site factors that influence moisture conditions within the stands influenced, the acuteness and direction of anatomical changes in the stemwood.

Keywords: Wood cellular anatomy; dendroecology; *Pseudotsuga menziesii*; *Choristoneura occidentalis*; herbivory; environmental factors; radial cell diameter, latewood cell wall thickness; wood density; drought tolerance

5.3 Introduction

Western spruce budworm (*Choristoneura occidentalis* Freeman; WSB) is a native defoliator of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) and true firs (*Abies* spp.) throughout western North America (Furniss and Carolin 1977). In British Columbia (B.C.) systematic surveys did not begin until the late 1940s (Harris et al. 1985), however, it is estimated nearly half of the 44,731 km^2 area that comprises the interior Douglas-fir zone (Meidinger and Pojar 1991) has been defoliated at least once by WSB outbreaks (Maclauchlan and Brooks 2009). Tree-ring reconstructions of WSB outbreaks over multiple centuries in B.C. indicate that outbreaks have a return interval of ~30 years (Campbell et al. 2006, Alfaro et al. 2014), with an average outbreak duration of 11 to 15 (Axelson et al. 2015). While there has been no apparent change in WSB outbreak frequency over the 20th and 21st centuries (Alfaro et al. 2014), a sustained outbreak that began in the late 1990s in southern B.C. interior is only now beginning to collapse (Buxton and Maclauchlan 2014, Westfall and Ebata 2014).

The interior Douglas-fir zone has historically been an important source of timber for the manufacturing of high quality structural products. Most southern stands were selectively logged in the early part of the 20th century, which consisted to removing the majority of the largest and most valuable trees (Smith 1962). Commercial logging activity, combined with fire protection and cattle grazing, has resulted in forests that have heterogeneous age and size structure, and that are highly susceptible to defoliation by WSB larvae (Maclauchlan and Brooks 2009). Repeated WSB outbreaks, especially those that are sustained, result in large timber volume losses, stem defects, mortality primarily in understory trees, and regeneration delays due to budworm feeding on developing cones (Alfaro et al. 1982, Alfaro and Maclauchlan 1992, Maclauchlan and Brooks 2009).

Defoliation causes radial growth suppression (i.e., defoliated trees produce narrow annual rings) resulting in declines in volume (Alfaro et al. 1982, Waring 1987, Thomson and Alfaro 1990, Swetnam and Lynch 1993). At the cellular level it has been demonstrated that during WSB outbreaks, Douglas-fir stemwood has significantly lower annual percent latewood, reduced cell wall thickness, and reduced cell diameters (Axelson et al. 2014).

Variations in anatomical characteristics can be mediated by a number of environmental factors including drought (Martinez-Meier et al. 2009, Rais et al. 2014), disease (Johnson et al. 2005), fire injury (Bigio et al. 2010, Arbellay et al. 2012), insect herbivory (Filion and Cournoyer 1995, Franceschi et al. 2005, Axelson et al. 2014, Copini et al. 2014), thinning and fertilization (Brix and Mitchell 1980), and air pollution (de Kort et al. 1991, de Kort 1993). Prior research on the anatomical and cambial characteristics of Douglas-fir focused on the physiological response to drought (Domec and Gartner 2002, Martinez-Meier et al. 2008, Martínez-Cabrera et al. 2009, Dalla-Salda et al. 2009, Rais et al. 2014, Ruiz Diaz Britez et al. 2014). Douglas-firs that survived the European drought of 2003 had significantly higher mean stemwood density, mean ring density, maximum ring density, latewood density and percent latewood (Martinez-Meier et al. 2008). During periods of low soil moisture, Domec and Gartner (2002) suggest that the main stem of mature Douglas-fir trees plays an adaptive role in preserving the whole tree from xylem embolism which can lead to hydraulic failure.

The objective of this study was to evaluate the combined role of climatic variability and chronic WSB defoliation on the anatomical characteristics in the stemwood of uneven-aged interior Douglas-fir trees located in the xeric southern interior of B.C. For this, we constructed ring-width chronologies and earlywood and latewood tracheid chronologies. We hypothesized that: 1) growing season climatic variability, particularly precipitation, and WSB defoliation severity and duration affects wood anatomical characteristics; and, 2) canopy class mediates anatomical characteristics due to competitive effects in structurally complex stands. These research findings contribute to our understanding of the affects of climatic variability, insect herbivory, and stand competition on stemwood cellular characteristics of uneven-aged interior Douglas-fir.

5.4 Study area

The study was conducted on Douglas-fir trees located at two permanent research plots established by Dr. Vince Nealis (Pacific Forestry Centre, Victoria B.C.) in 1997 to evaluate the dynamics of local WSB populations (Nealis et al. 2009). The sites are located within the Nicola Valley on the Thompson Plateau in the southern B.C. (Fig. 5.1). The stands are positioned within the interior Douglas-fir biogeoclimatic zone, in low to mid-elevation landscapes dominated by Douglas-fir forests. Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) is common, as is interior spruce (*Picea engelmannii* Parry ex Englem.) in the wetter parts of the zone, and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) in the hottest and driest areas of the zone (Lloyd et al. 1990).

Site 3 is positioned on a moderate slope (< 5°) with an aspect of 110° at 1050 m asl (50°13’ 17” N; 120°39’ 03” W; Fig. 5.1) in a xeric-hot subzone (Lloyd et al. 1990). The site is characterized by open multi-storied Douglas-fir forest (~ 490 trees/hectare), with an understory dominated by a thick cover of pinegrass (*Calamagrostis rubescens*) and moderate amounts of kinnikinnick (*Arctostaphylos uva-ursi*).

Site 4 is situated above Site 3 on flat to gently rolling terrain at 1350 m asl (50°14’11” N; 120°39’43” W; Fig. 5.1) in the dry-cool subzone (Lloyd et al. 1990). A dense multi-storied Douglas-fir forest characterizes the site (~560 to 900 trees/hectare), with an intermediate layer of interior spruce and regenerating lodgepole pine. The understory contains a low cover of pinegrass, moderate amounts of birch-leaved spirea (*Spiraea betulifolia*), soopolallie (*Shepherdia canadensis*), and heart-leaved arnica (*Arnica cordifolia*), and a minor component of twinflower (*Linnaea borealis*) and kinnikinnick. The species composition and the dry-cool subzone classification indicate that Site 4 experiences wetter and cooler conditions than Site 3.

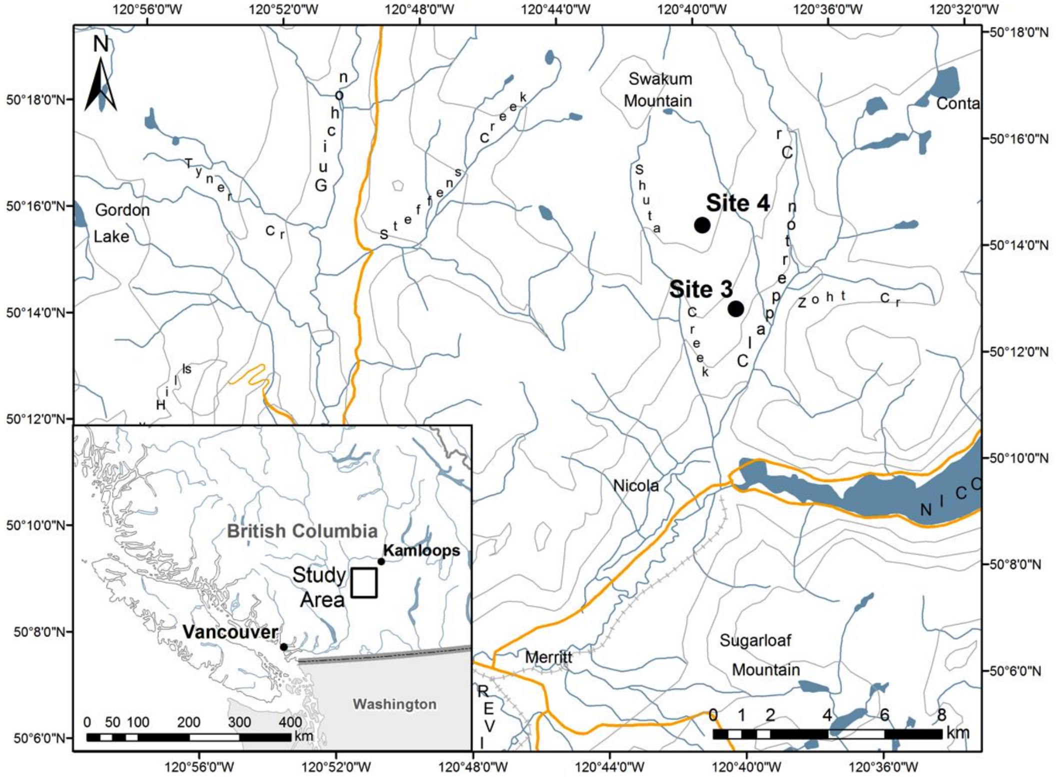


Figure 5.1 Location of study sites used to examine the relationship between western spruce budworm defoliation and anatomical characteristics in the wood of Douglas fir. The sites are approximately 15 km northeast of Merritt in the Nicola Valley, southern interior of British Columbia, Canada.

The local climate of the interior Douglas-fir zone is characterized by warm dry summers, a fairly long growing season, and cool winters with low to moderate snowfall. Frosts are common in early June and in late August, and substantial moisture deficits occur throughout the growing season (Lloyd et al. 1990). Interpolated ClimateWNA data (ClimateBC, v4.71; Wang et al. 2006, 2012) was used to create a regional record (see section 5.6.1). Climate normal data, 1981-2010, (Fig. 5.2) indicate that the mean annual temperature in the study area is 4.5°C, with spring and summer temperatures averaging 4.4°C and 14°C, respectively, and maximum spring and summer temperatures average 10.4°C and 21°C, respectively (Fig. 5.2). Annual precipitation in the study area is very low (~388 mm), which is near the lower precipitation limit that Douglas-fir can withstand before being replaced by ponderosa pine as the dominant species (Pfister et al. 1977, Silen 1978, Lloyd et al. 1990). Of the 388 mm of annual precipitation, 33% occurs in the fall and winter seasons primarily as snow while the other 27% occurs as rain from May through July. Average May, June, and July precipitation is 35.5 mm, 35.3 mm and 34.1 mm, respectively (Fig. 5.2).

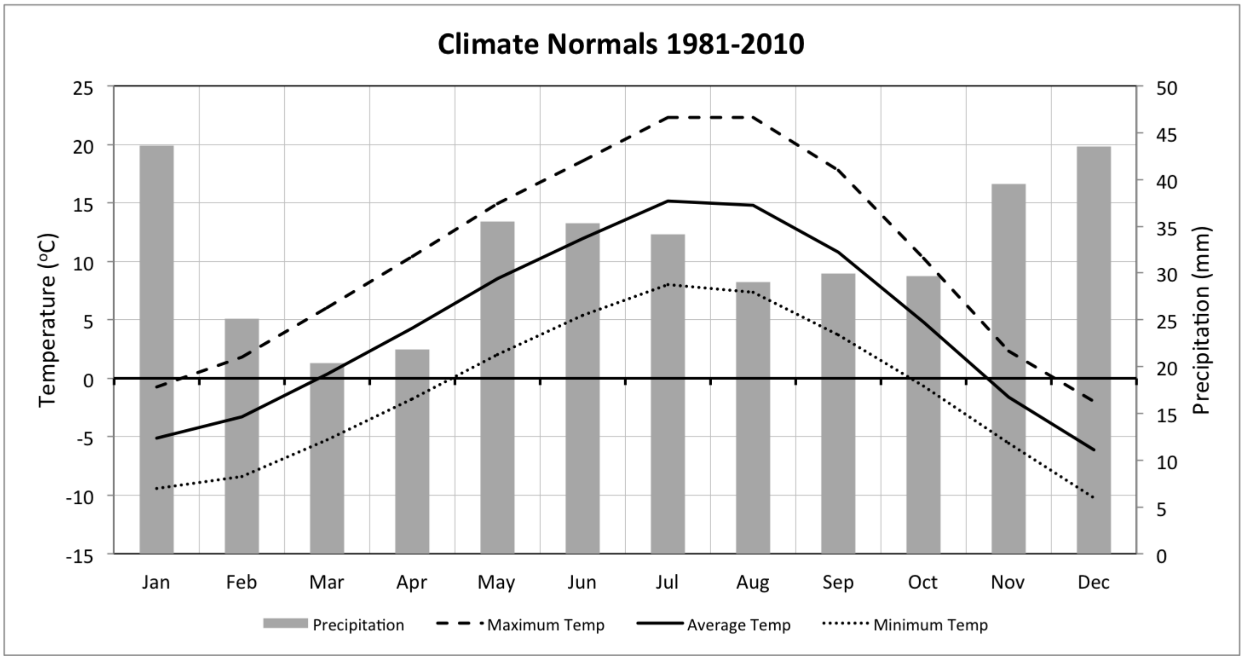


Figure 5.2 Regional climate normal data (1981-2010) for monthly precipitation and temperature variables from interpolated ClimateWNA data (Wang et al. 2012) (see section 5.6.1) in the Nicola Valley, southern interior of British Columbia, Canada.

5.5 Field and laboratory methods

5.5.1 Field procedures

Increment cores samples were collected at both study sites in August 2012. Two 5.2 mm cores were extracted per tree from 25 trees per site, one at stump height (30 cm above ground) and a second at breast height (1.3 m above ground). A third increment core was collected at breast height, opposite the first coring site and parallel to the slope contour, with a 12 mm borer. Diameter-at-breast height (DBH) was measured and the canopy position was recorded for each sampled tree. Three canopy classes were recorded: Dominant (D) - the tallest trees of the main canopy, including veterans (i.e., the oldest trees in the stand that have often survived past disturbances such as wildfire), receiving direct sunlight on aspects of the crown; Co-dominant (CD) - main layer of trees whose crowns form the upper layer of foliage but receive direct sunlight only on the top of the crown; and Intermediate (I) - distinct secondary canopy of trees of various heights, younger than those in the main canopy. Intermediate trees receive light filtered by the upper canopy trees (Province of British Columbia 2010).

At the time of sampling Site 3 had sustained extensive stand-level, and severe tree-level defoliation in that and previous years, as evidenced by very low foliage biomass. Abundant overstory trees with topkill, and low frequency of saplings, indicated the stand vigour was low. At Site 4 the intensity of WSB feeding was much less than at Site 3, with less prevalent topkill and saplings that exhibited moderately good vigour and more crown biomass.

5.5.2 Laboratory procedures

Tree-ring chronologies were developed using standard dendrochronological methodologies (Stokes and Smiley 1968). Polished tree ring samples were measured with WinDendro (Ver. 2009d, Regents Instruments Inc. 2009) at a precision of 0.01 mm, and subsequently visually crossdated and verified using COFECHA (Holmes 1986) to ensure exact calendar years were assigned to each tree ring. Individual ring-width series were standardized using a negative exponential curve to remove biological and geometric growth trends (Cook et al. 2007). Stand-level chronologies were developed using a bi-weight robust mean that minimizes the effect of outliers and produces a dimensionless stationary index with a defined mean of 1.0 (Cook and Kairiukstis 1990).

For anatomical measurements the 12 mm cores were cut into 5-6 cm long segments starting from the 1995 or 1996 annual ring to the bark. Core segments were split radially and micro sections cut on the cross-sectional plane using a GSL1 microtome equipped with removable NT-cutter blades (Gärtner et al. 2014). Micro sections were cut to a thickness of 15 µm using a non-Newtonian fluid to reduce preparation problems related to the separation of secondary cell walls and cell distortion (Schneider and Gärtner 2013). Micro sections were double stained with cellulose and lignin specific dyes (Astrablue and Safranin), dehydrated with alcohol, rinsed in Xylol and embedded in Canada balsam (Gärtner et al. 2013). Permanent slides were photographed with a digital camera system, Colorview IIIu camera mounted on an Olympus BX41 microscope, at 40x magnification.

Twenty micro sections were measured (e.g., Fig. A1) using WinCell (Ver. 2004a, Regents Instruments Inc. 2004). Up to fifteen annual rings were measured (1997-2011) (e.g., Figs. A4 and A5) along 8-14 radial files per ring on each sample (Axelson et al. 2014). The following parameters were recorded for earlywood and latewood tracheids: cell lumen area (µm^2); cell wall thickness (µm); and, radial cell diameter (µm), and percent latewood (%). Data for each tree was separated into earlywood and latewood components and radial files were averaged per year by tree

5.6 Analytical methods

Of central interest in this study is how a number of environmental factors: climate, insect herbivory and stand-level competition, affects the stemwood cellular anatomy of interior Douglas-fir. Major challenges arose from the anatomical datasets themselves, and disentangling the influences of the environmental factors on the cellular characteristics examined. All statistical analyses were completed using the software *R* (Ver. 3.0.2, R Core Team 2013).

5.6.1 Dendroclimate analysis

To determine what suite of climatic variables were appropriate to use in anatomical analysis we explored climate – radial growth relationships. Site-specific climate data was not available for this study, so climate variables were derived using the software ClimateBC (v4.71; Wang et al. 2006, 2012), which interpolates ClimateWNA regional climate and historical anomaly data through a combination of bilinear interpolation and elevation adjustments to generate site-specific climate estimates (Wang et al. 2012). Derived climatic data were obtained by draping an ArcGIS (Ver.10.1, ESRI) grid over the study sites and adjacent areas in the interior Douglas-fir zone. The grid produced 50 interpolated climate datasets that were averaged to produce a single regional record for climate normal data (1981-2010), and for monthly and seasonal climate variables (1901-2012).

The effects of climate on tree radial growth were evaluated with 20-year moving window Pearson correlation coefficients with 5-year overlaps between standardized residual chronologies and averaged climatic variables: monthly minimum; mean and maximum temperatures; and, precipitation using the *dcc* function in the *treeclim* package (Zang and Biondi 2015a). The *dcc* function performs bootstrap resampling (1000 iterations) to test for significant correlations (Zang and Biondi 2015b), and moving window correlations assess the stability of correlations over time.

We were specifically interested in how early growing season climate variables influenced anatomical characteristics. In Douglas-fir, cambial reactivation following winter dormancy starts with radial expansions of cells, in mid- to late February (Dodd and Fox 1990, Fielder and Owens 1989). Foliar buds begin expanding around late March, and bud burst starts as early as April in the coastal zone (Owens 1968). These dates are likely early for the interior Douglas-fir growing at our study sites, so we included two seasonal variables: spring (March – May) maximum temperature (^{o}C) and total precipitation (mm). It is reasonable to expect that by late April to early May that Douglas-fir at our study sites would be undergoing radial expansion of cells and bud burst, auxin movement from expanding buds to the cambium (Larson 1962), and xylem development.

5.6.2 Defoliation analysis

To evaluate how a chronic WSB outbreak influences Douglas-fir stemwood cellular characteristics we accessed defoliation data collected by Dr. Vince Nealis

(Pacific Forestry Centre, Victoria B.C). Trees at the two sites have been monitored for defoliation since 1997, with the annual survey based on late summer current-year foliage (Vince Nealis *personal communication*). Different trees were sampled mid-crown over the 15-year measurement window due to branch accessibility and/or availability. Each year, one 45 cm branch from 10 trees per stand were collected, and twenty-five randomly selected shoots on each branch were assessed (Nealis et al. 2009) and characterized for defoliation using the following classes: 1: no defoliation; 2: 1-25%; 3: >25-50%; 4: >50-75%; 5: >75-100% (Fettes 1950).

To establish the annual defoliation history at the stand level we calculated the median defoliation categories for every year at both sites. Median stand-level defoliation severity (Fettes) at Site 3 indicated that 10 out of the 15 years recorded >75% crown defoliation (Fig. 5.3). The median stand-level defoliation at Site 4 indicated that budworm feeding intensity was variable: from 1997 to 2002 defoliation ranged from zero to a maximum of 50% crown defoliation, and only 4 of 15 years had >75% crown defoliation (Fig. 5.3).

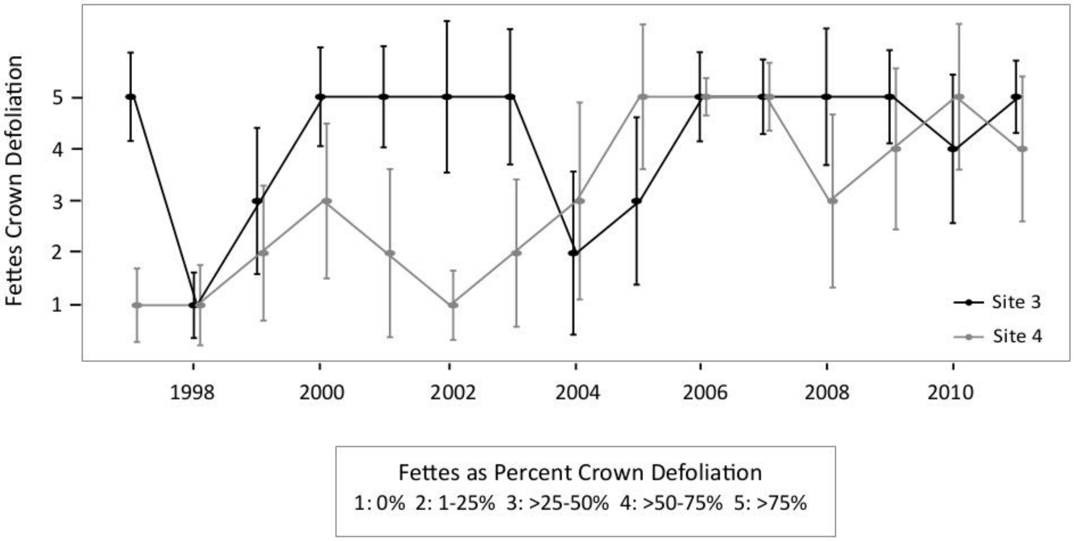


Figure 5.3 Annual median defoliation (± standard deviation) from 1997 to 2011 at Sites 3 and 4 in the Nicola Valley, southern interior of British Columbia, Canada (Data provided by Dr. Vince Nealis, Pacific Forestry Centre, Victoria B.C.).

WSB outbreak duration has been shown to be an important component of outbreak dynamics and subsequent impacts on host trees (Alfaro et al. 1982). We created a cumulative defoliation variable that counted consecutive years of measured defoliation (Fettes $\geq$ 2). Cumulative defoliation at Site 3 ranged from zero (1998) to a maximum of thirteen years (1999-2011) of continuous budworm feeding (Fig. 5.3). Cumulative defoliation at Site 4 ranged from zero to a maximum of nine years (2011) of continuous budworm feeding (Fig. 5.3), with three years had no budworm feeding (1997-98 and 2002) (Fig. 5.3).

5.6.3 Anatomical analysis

The anatomical datasets measured provide some analytical challenges. For one, there is the potential problem of pseudoreplicaton. For each tree, multiple radial files were measured per annual growth ring. We needed a solution that would recognize the dependence among the measured annual growth rings on a tree and consider that multiple radial files act as subsamples rather than true replicates. Our approach was to average data over the sub-samples and to analyze the average only (Hurlbert 1984). With numerous measurements in each growth year per tree (8 to 14 radial files), a robust average for earlywood and latewood anatomical variables per ring was developed at each site.

To overcome the problems arising from anatomical datasets that were: 1) hierarchical (multiple measurements per tree), 2) imbalanced (unequal number of trees sampled in a given year), and 3) autocorrelated (consecutive years measured on the same trees) we used linear mixed effects (LMEs) models (Pinheiro and Bates 2000) with the *gls* and *lme* functions in the *nlme* package (Pinheiro et al. 2015). We evaluated numerous models to predict anatomical variables, as follows: a) no random effect, b) no correlation structure, c) no random effect or correlation structure, d) different predictor variables (including the intercept) as random effects, e) various R-side correlation structures, and f) various two-way interaction terms. Models were compared with likelihood ratio tests, and final model selection was based on those that demonstrated the lowest Akaike

Information Criteria (AIC), an information-theoretic model selection procedure that measures the goodness-of-fit (Bolker et al. 2009, Zurr et al. 2009). LMEs were fit using restricted maximum-likelihood (REML) estimation, and within-subject (among-year) correlation was specified with a first-order autoregressive model (AR1).

The LME took the following form for each tree, $i = 1, 2, \dots n$, with independence assumed among them:

$$\boldsymbol{y}_i = \mathbf{X}_i \boldsymbol{\beta} + \mathbf{Z}_i \boldsymbol{b}_i + \boldsymbol{\varepsilon}_i \tag{1}$$

Where $\boldsymbol{y}_i$ is the m_i-dimensional response vector for each tree, $\boldsymbol{\beta}$ is the p-dimensional vector of fixed effects, $\boldsymbol{b_i}$ is the q-dimensional vector of random effects, $\mathbf{X}_i$ and $\mathbf{Z}_i$ are known fixed-effects and random effects design matrices, and $\boldsymbol{\varepsilon}_i$ is the error vector (Eqn. 1) (Pinhiero and Bates 2000). The AR(1) modeled residual error took the following form:

$$\varepsilon_{it} = \phi_1 \varepsilon_{i(t-1)} + \eta_{it} \tag{2a}$$

$$\eta_{it} \sim N(0, \sigma^2) \tag{2b}$$

Where ϕ_1 is the autoregressive parameter, i is the index for the tree and t is the index for the years $t = 1, 2, \dots, m_i$ (Eqn. 2a). The η_{it} are independent normally distributed random variables with mean 0 and variance σ^2 (Eqn. 2b). The overall covariance matrix for $\boldsymbol{\varepsilon}_i$ for the AR(1) was:

$$\sigma^2 \begin{bmatrix} 1 & \rho & \rho^2 & \rho^3 \\ \rho & 1 & \rho & \rho^2 \\ \rho^2 & \rho & 1 & \rho \\ \rho^3 & \rho^2 & \rho & 1 \end{bmatrix} \tag{3}$$

Model fit for each response variable was assessed visually with graphical validation plots (Zuur et al. 2009), including: residuals versus fitted values to verify homogeneity; QQ-plot and histograms of the residuals to verify normality; and, autocorrelation and partial autocorrelation plots of the model residuals to detect possible patterns in autocorrelation (Bates and Pinheiro 2000, Zuur et al. 2009). A marginal ANOVA (i.e., type III sum of squares), computed from Wald chi-square tests for each fixed effect, provided a single overall test of the usefulness of a given explanatory variable, without focusing on individual levels. The package *effects* was used to produce partial-residual plots (Fox 2015), which show the partial relationship between the anatomical parameter and the significant predictors with the effects of the other predictors present. Partial-residual plots reveal whether the data support the specified form of the model; the extent and direction of linearity, and the extent and deviation from linearity (Larsen and McCleary 1972, Cook 1993). To test for significant differences between categorical variables, canopy class and defoliation severity (Fettes), and anatomical characteristics we conducted post-hoc testing of individual levels with least-squares means using a pairwise comparison and Tukey's adjustment ($p<0.05$) with the package *lsmeans* (Lenth and Hervé 2015).

5.7 Results

5.7.1 Dendrochronology

Trees began colonizing the two sites in the late 1890s (Site 3) and early 1880s (Site 4), with mean establishment years of 1922 (Site 3) and 1928 (Site 4). Crossdating was robust, with inter-series correlations of 0.71 at Site 3, and 0.67 at Site 4, and first-order autocorrelation was 0.66 at both sites (Table 5.1).

The standardized chronologies had numerous periods of below average growth, and sites experienced major growth release events in the 1960s at Site 4, and in the 1980s at both sites (Fig. 5.4a). These releases were likely resulted from timber harvesting that removed the largest trees (Smith 1962, Klenner et al. 2008). Excluding these release events, radial growth tended to be below average (<1.0) over much of the record, particularly from 2003 to 2011 (Fig. 5.4a). From 1997 to 2011, during the WSB outbreak

Table 5.1 Tree ring properties of Site 3 and 4 in the Nicola Valley, southern interior of British Columbia, Canada.

Site	Length of Master	Mean year of tree establishment [a] ± SD	Inter-series *r*	Number of dated series	AC [b]
Site 3	1896-2011	1922 ±17.8	0.709	50	0.66
Site 4	1882-2011	1928 ±15.3	0.675	50	0.66

[a] Mean year of establishment based on crossdated cores collected at stump height (0.3m).

[b] First order autocorrelation

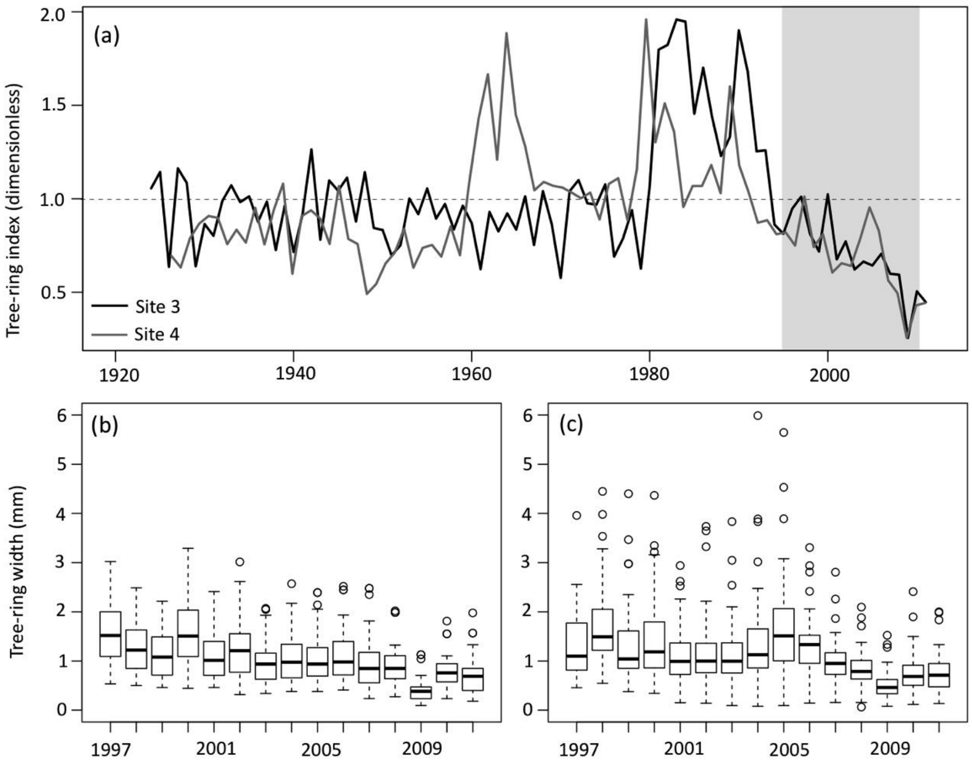


Figure 5.4 Annual radial growth increment for sites sampled in the Nicola Valley: a) standard chronologies truncated to average establishment year (Table 5.1) for Site 3 (black line) and Site 4 (grey line). Grey shading shows the defoliation measurement period (1997-2011), horizontal dashed line is chronology mean of 1.0; b) Site 3 raw tree ring growth (mm); c) Site 4 raw tree ring growth (mm). Boxes represent the interquartile range and median, whiskers indicate the variability outside the upper and lower quartiles, and outliers are plotted as individual points.

variability in radial growth was similar between sites (Fig. 5.4a). At the tree-level, raw annual increments were similar, averaging ~1 mm/year. Annual growth decreased below this after 2000 at Site 3 and after 2006 at Site 4, and the tree ring formed in 2009 recorded the smallest growth increment in the 15-year period (Figs. 5.4b and 5.4c). While overall median growth was similar between the sites, at Site 4 there was more variability in individual tree growth evidenced by growth outliers (Fig. 5.4c), suggesting the trees at this site location experienced better growing conditions.

5.7.2 Stand structure

Stand structure at both sites was heterogeneous, nevertheless size and age structure were similar between sites (Table 5.2). Average tree age and age ranges were similar for the dominant (D) canopy class between sites; in the co-dominant (CD) canopy class the trees were older than the D trees at Site 3; in the intermediate (I) crown class average age was nearly the same between sites, but a greater range of ages were present in Site 3 than Site 4 (Table 5.2).

Table 5.2 Summary of stand structure data from Site 3 and Site 4 in the Nicola Valley, southern interior of British Columbia, Canada.

Crown Class	DBH [a] ± SD	Age ± SD	Age Range	*N* [b]
Site 3				
Dominant	42 ± 4.4	89 ± 14.7	74 - 104	0.34
Co-dominant	30.8 ± 3.3	96 ± 12.4	84 - 108	0.44
Intermediate	22.2 ± 4	75 ± 24.3	52 - 98	0.22
Site 4				
Dominant	45.8 ± 5.8	90 ± 17.3	73 - 107	0.20
Co-dominant	32 ± 3.1	82 ± 14.7	67 - 97	0.50
Intermediate	23.3 ± 1.9	76 ± 9.7	66 - 86	0.30

[a] Diameter at breast height (cm) measured at 1.3 m.
[b] Proportion of trees sampled in each canopy class

5.7.3 Climate relationships

The strongest and most temporally stable climate-growth relationships were with monthly maximum temperature and monthly precipitation (Fig. 5.5). Relationships with monthly average temperature were similar but weaker, and were seldom significant with monthly minimum temperature (results not shown). At Site 3, tree growth was negatively correlated to May and June maximum temperature, with the strongest and most temporally stable relationship in June. Tree growth was positively correlated to May through July precipitation, and negatively correlated with March precipitation for a brief period (1947-1966) (Fig. 5.5). At Site 4, correlations with climatic variables were weaker than at Site 3, though the general patterns were similar (Fig. 5.5). At Site 4, tree growth was negatively correlated to June and July maximum temperature, although this relationship is temporally variable (Fig. 5.5). Tree growth was positively correlated with July precipitation, although these relationships were not significant after the early 1990s, and negatively correlated with March precipitation from 1937 to 1966 (Fig. 5.5).

Climatic variability for maximum spring temperature, total spring precipitation, and average June and July precipitation from 1996 to 2012 shows a range of above and below average values, computed from the long-term mean (1901-2012) (Fig. 5.6). During this period, maximum spring temperature had six years that were above average, particularly from 2004 to 2007 (Fig. 5.6). Spring precipitation was characterized by above average conditions from 1996 to 2012, with the wettest year occurring in 1996 and the driest in 2012 (Fig. 5.6). June precipitation, which had the strongest positive correlations with tree-ring chronologies at each site, was characterized by above average values from 1996 to 2002 and then a period of sustained below average precipitation until 2012, which was similar for July precipitation (Fig. 5.6). For June precipitation the driest years occurred in 2009, 2011 and 2002, and for July precipitation the driest years occurred in 2010, 2003 and 2006 (Fig. 5.6).

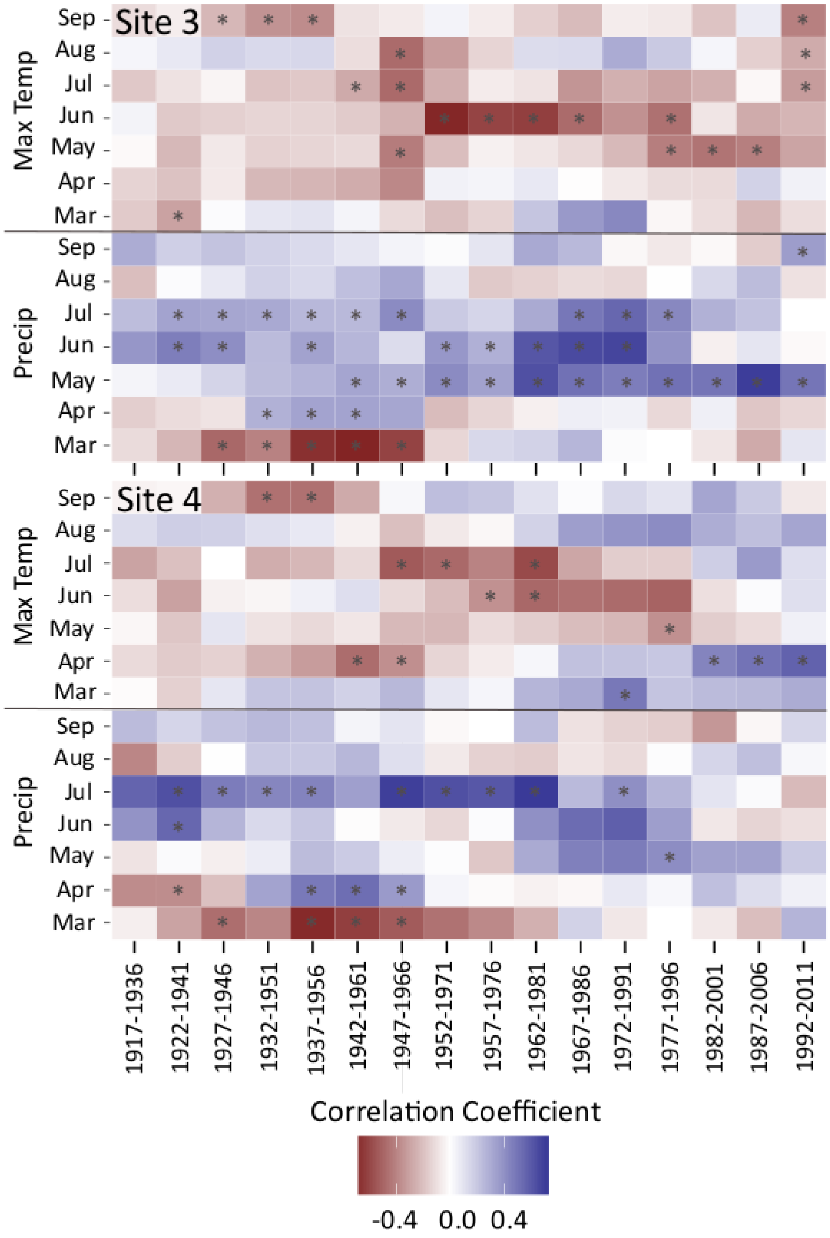


Figure 5.5 Moving window (20-year window with 5-year overlap) Pearson correlation coefficients between Site 3 (top) and Site 4 (bottom) residual chronologies and monthly average maximum temperature (°C) and monthly total precipitation (mm) from May through September of the current growing year. Grey asterisk indicates significant (p<0.05) correlations, and degree of shading indicates strength of the correlation coefficient.

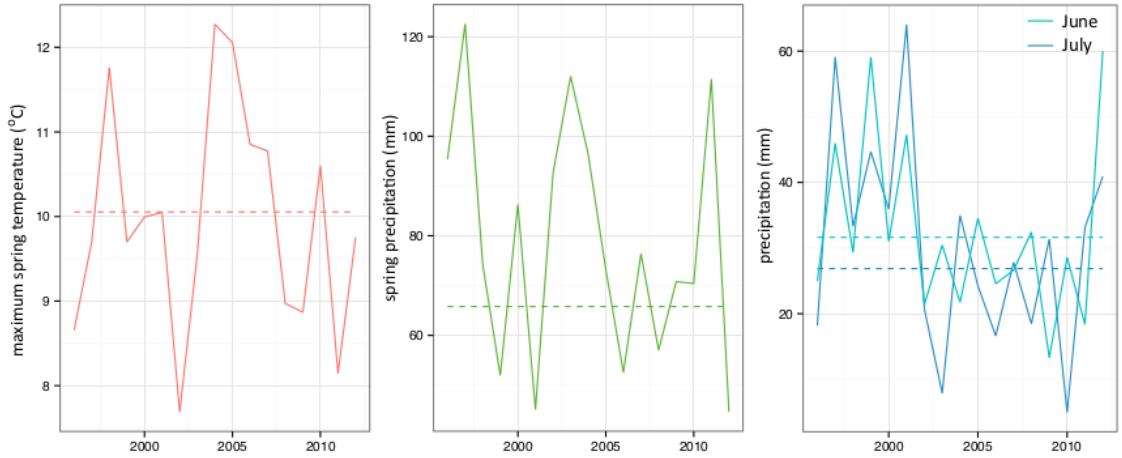


Figure 5.6 Climate variables: maximum spring temperature (left), total spring precipitation (middle), and average June and July precipitation (right) from 1996 to 2012 (hashed line is the mean (1901-2012)) from regional climate dataset derived for the study area (see 5.6.1) in the Nicola Valley, southern interior of British Columbia, Canada.

5.7.4 Anatomical characteristics

We developed annually resolved tree-level cellular anatomical datasets for a number of earlywood and latewood tracheid features over a 15-year period at each site. Sample size was robust for the entire time period at both sites, see Appendix I for sample depth and summary statistics averaged by year (Tables A7 to A12). Earlywood and latewood variables were graphed based on their canopy class positions (Figs. 5.7 to 5.9), with a locally weighted regression smoothing spline to highlight the original data points and the standard error of the smoothed surface (Wickham and Chang 2013). For earlywood variables, lumen area and radial cell diameter had increasing trends over time, especially at Site 3 (Fig. 5.7). For latewood tracheids cell wall thickness, radial cell and percent latewood had decreasing trends over time at Site 3 and oscillated at Site 4 (Figs. 5.8 and 5.9). There were visual differences between crown classes, especially for earlywood lumen area and earlywood radial cell diameter (Fig. 5.7); tracheids from the D trees had the largest values, tracheids from the I trees had the smallest values (values of the CD trees were similar to those in the D canopy class) (Figs. 5.7 to 5.9).

To determine how much each anatomical variable changed (independent of canopy class), the percentage difference was calculated between minimum and maximum values for anatomical variables. At Site 3, earlywood lumen area and earlywood radial cell diameters increased by 25% and 20%, respectively (Fig. 5.7; Table A7). Latewood cell wall thickness, latewood radial cell diameter and percent latewood decreased by 28%, 23% and 43%, respectively (Figs. 5.8 and 5.9; Tables A8 and A9). At Site 4, earlywood lumen area and earlywood radial cell diameter lacked a clear trend, though overall percentage increases were 11% and 8%, respectively (Fig. 5.7; Table A10). Latewood cell wall thickness, latewood radial cell diameter and percent latewood oscillated over the 15-year measurement window (Fig 5.8 and 5.9); percentage decreases were 23%, 18% and 33%, respectively (Tables A11 and A12). Latewood lumen area stayed relatively constant over the 15-year period at both sites, consistent with the findings of Axelson et al. (2014), however, it was interesting to note that lumen area at Site 3 were considerably smaller, averaging around 100 μm^2 compared to Site 4, where lumen area averaged around 150 μm^2 (Fig. 5.8).

5.7.5 Anatomical modeling

Earlywood and latewood anatomical variables were modeled using a number of fixed effects, including: tree level canopy class, stand level defoliation (severity and cumulative), and a number of climatological variables (Table 5.3), and included a random intercept with trees as the subject (Table 5.3). Reduced models (see 5.6.3) had higher log likelihood values and higher Akaike Information Criterion (AIC) values demonstrating that inclusion of a random effect and correlation structure were important features of the final model. Models with two-way interactions: canopy class and defoliation severity and

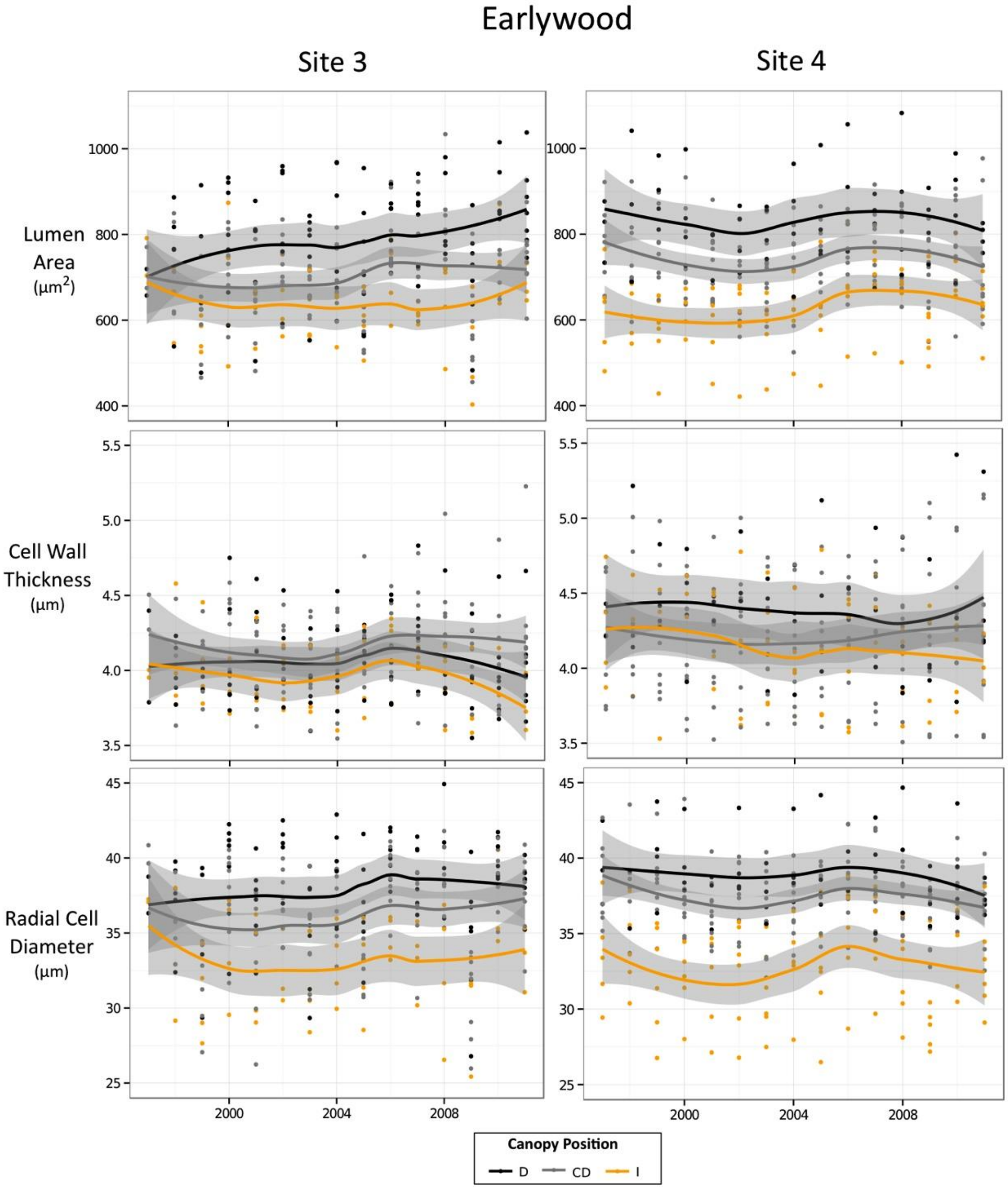


Figure 5.7 Earlywood anatomical variables fit with a locally weighted regression, at Site 3 (left) and Site 4 (right). Lumen area (top), cell wall thickness (middle), and radial cell diameter (bottom) graphed by canopy class (Table 5.2): Dominant (black), Co-dominant (gray) and Intermediate (orange).

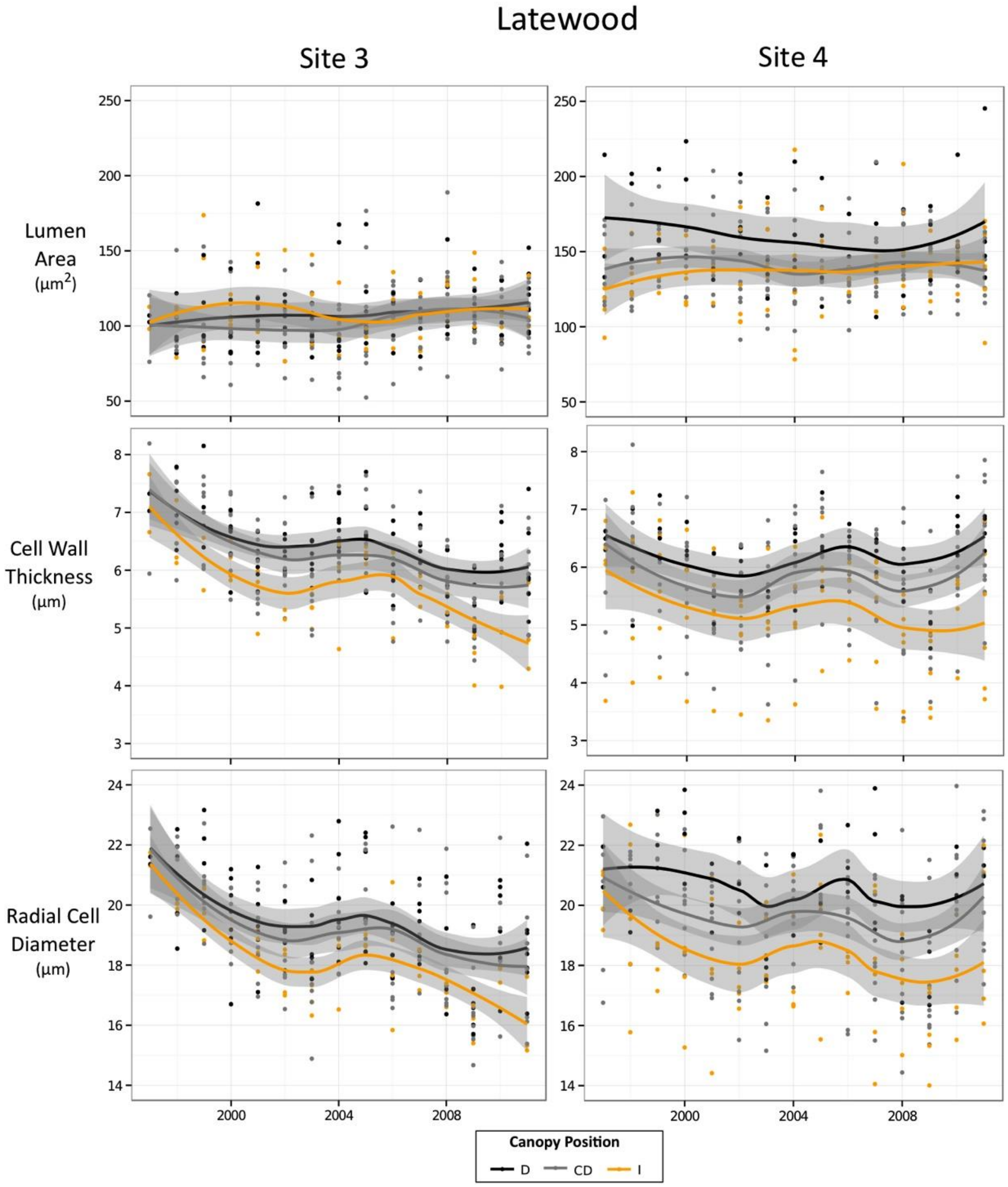


Figure 5.8 Latewood anatomical variables fit with a locally weighted regression, at Site 3 (left) and Site 4 (right). Lumen area (top), cell wall thickness (middle), and radial cell diameter (bottom) graphed by canopy class (Table 5.2): Dominant (black), Co-dominant (gray) and Intermediate (orange).

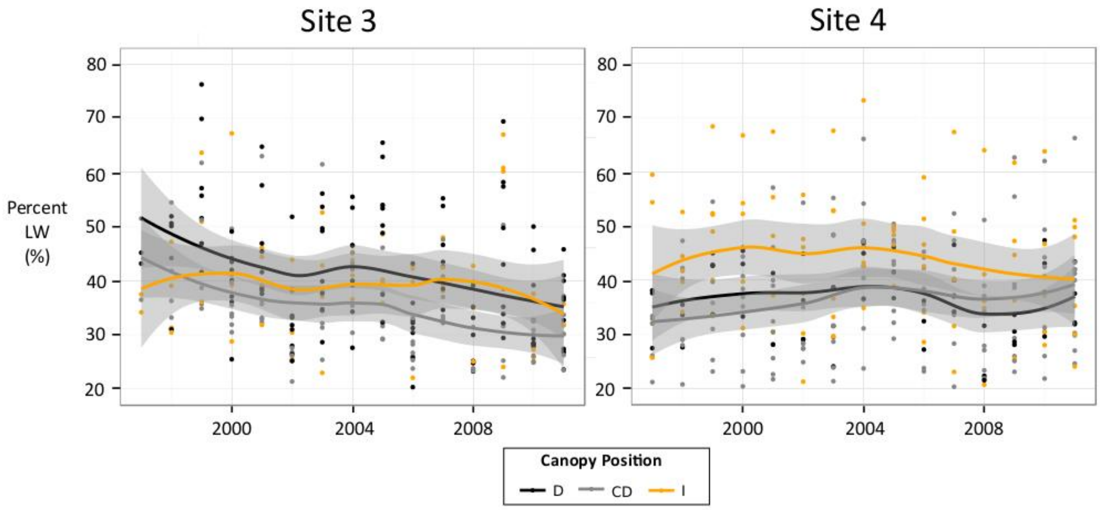


Figure 5.9 Percent latewood fit with a locally weighted regression, at Site 3 (left) and Site 4 (right). Lumen area (top), cell wall thickness (middle), and radial cell diameter (bottom) graphed by canopy class (Table 5.2): Dominant (black), Co-dominant (gray) and Intermediate (orange).

canopy class and cumulative defoliation, increased AIC values and were not significant, therefore excluded from the final models. Examination of the final model residuals indicated that the assumptions of normality, homogeneity and independence were not violated. Exceptions to this were at Site 3 for earlywood radial cell diameter, latewood lumen area, and percent latewood; and at Site 4 for latewood lumen area. In these instances residuals deviated slightly from the normality assumption.

The results of the ANOVA for each anatomical parameter provided a single test of the power of explanatory variables used in the models (Tables 5.4 and 5.5). Partial-residual plots indicated that relationships between anatomical parameters and continuous fixed effects (i.e., cumulative defoliation and climate variables) were generally linear, and illustrated the relationship between the anatomical parameter and the significant fixed effects in each model (Figs. 5.10 to 5.19).

Table 5.3 Response variables, random effect, and fixed effects used to develop site specific linear mixed effect models for anatomical characteristics of interior Douglas-fir located in the Nicola Valley, southern interior of British Columbia, Canada.

Name	ID	Structure	Unit/description
Response Variables			
Early- and latewood lumen area	LA	Numeric	Micrometers^2 (μm^2)
Early- and latewood cell wall thickness	CWT	Numeric	Micrometers (μm)
Early- and latewood radial cell diameter	RCD	Numeric	Micrometers (μm)
Percent latewood	LW_P	Numeric	Percentage (%)
Random Effect			
Tree		Factor	20 sample trees per site
Fixed Effects			
Canopy class	CC	Factor	D=Dominant, CD=Co-dominant, I=Intermediate
Defoliation severity category	FET	Factor	1: 0%, 2: 1-25%, 3: >25-50%, 4: >50-75%, 5: >75-100%
Cumulative defoliation	CUM	Integer	0 for no defoliation (Fettes = 1), 1 up to 13 for consecutive years of defoliation (Fettes ≥ 2)
Max Temperature spring	MT_SP	Numeric	March – May Average Temperature (°C)
Precipitation spring	P_SP	Numeric	March – May Total Precipitation (mm)
Precipitation June	P_JUN	Numeric	Average Precipitation (mm)
Precipitation July	P_JUL	Numeric	Average Precipitation (mm)

Table 5.4 ANOVA results for Site 3, showing influence of model fixed effects on anatomical parameters in Douglas-fir forests of southern interior, British Columbia. Text in bold refers to significance effects (p<0.05).

Factor	Degrees of Freedom		Percent Latewood		Lumen area		Cell wall thickness		Radial cell diameter	
	Num	Den	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Earlywood										
CC	2	17	-	-	6.65	**0.007**	0.37	0.693	7.81	**0.004**
FET	4	236	-	-	5.13	**<0.0001**	1.06	0.376	7.29	**<0.0001**
CUM	1	236	-	-	3.54	0.061	1.22	0.269	5.09	**0.025**
MT_SP	1	236	-	-	3.67	0.056	4.64	**0.032**	29.16	**<0.0001**
P_SP	1	236	-	-	3.13	0.077	0.63	0.427	17.17	**<0.0001**
P_JUN	1	236	-	-	0.46	0.496	0.75	0.392	0.37	0.540
P_JUL	1	236	-	-	2.90	0.089	0.02	0.886	0.73	0.394
Latewood										
CC	2	17	3.08	0.079	0.36	0.700	3.49	0.053	1.87	0.184
FET	4	236	0.32	0.864	0.39	0.813	2.71	**0.031**	3.23	**0.013**
CUM	1	236	0.63	0.430	6.53	**0.011**	18.08	**<0.0001**	12.80	**<0.0001**
MT_SP	1	236	2.25	0.135	1.22	0.271	1.49	0.222	1.08	0.298
P_SP	1	236	1.68	0.196	1.68	0.196	20.05	**<0.0001**	12.95	**<0.0001**
P_JUN	1	236	4.43	**0.037**	1.41	0.236	14.33	**<0.0001**	17.81	**<0.0001**
P_JUL	1	236	5.60	**0.020**	0.14	0.703	0.03	0.856	0.47	0.491

Abbreviations: Num = numerator; Den = denominator; CC = canopy class; FET = defoliation severity (Fettes); CUM = cumulative defoliation; MT_SP = maximum spring temperature; P_SP = spring precipitation; P_JUN = June precipitation; P_JUL = July precipitation (Table 5.3).

At Site 3, earlywood lumen area was explained by canopy class and defoliation severity (Table 5.4). Pairwise comparisons of the means revealed that D-CD and D-I trees were significantly ($p<0.05$) different from one another, and that defoliation severity (Fettes) 3-4 and 3-5 were significantly ($p<0.01$) different from one another (Fig. 5.10). Earlywood radial cell diameter was most strongly predicted by maximum spring temperature and spring precipitation, followed by defoliation severity, canopy class and cumulative defoliation (Table 5.4); there was a positive trend between earlywood cell size and maximum spring temperature, spring precipitation, and cumulative defoliation (Fig. 5.11). Pairwise comparisons of the means revealed that defoliation severity (Fettes) 2-4, 2-5, 3-4, and 3-5 were significantly different from one another ($p<0.01$), and that D-I and CD-I canopy classes were significantly ($p<0.05$) different from one another (Fig. 5.11).

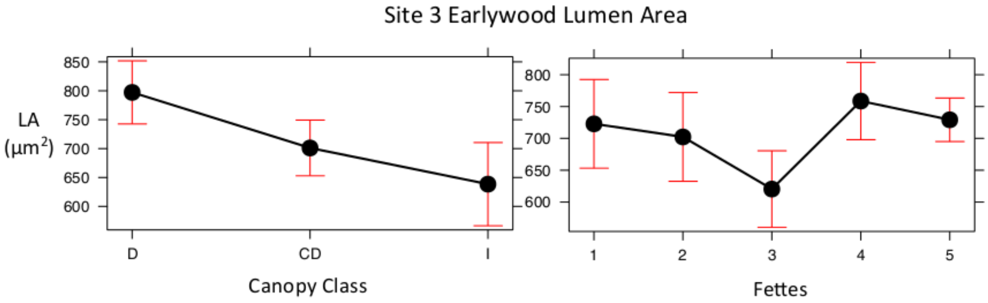


Figure 5.10 Site 3 earlywood lumen area with partial-residuals plotted on the scale of the original anatomical parameter on the vertical axis. Individual plots are arranged by highest *F* statistic and include only significant predictors (Table 5.4). The error bars on the categorical variables are the standard error of the estimate.

At Site 3, latewood lumen area was weakly predicted by a single variable, spring precipitation (Table 5.4). Latewood cell wall thickness was predicted by a number of fixed effects including spring precipitation, cumulative defoliation, June precipitation, and defoliation severity (Table 5.4); there were positive trends between latewood cell wall thickness and spring precipitation and June precipitation, and a negative trend between latewood cell wall thickness and cumulative defoliation (Fig. 5.12). Pairwise comparisons of defoliation severity (Fettes) indicated that differences in means were not

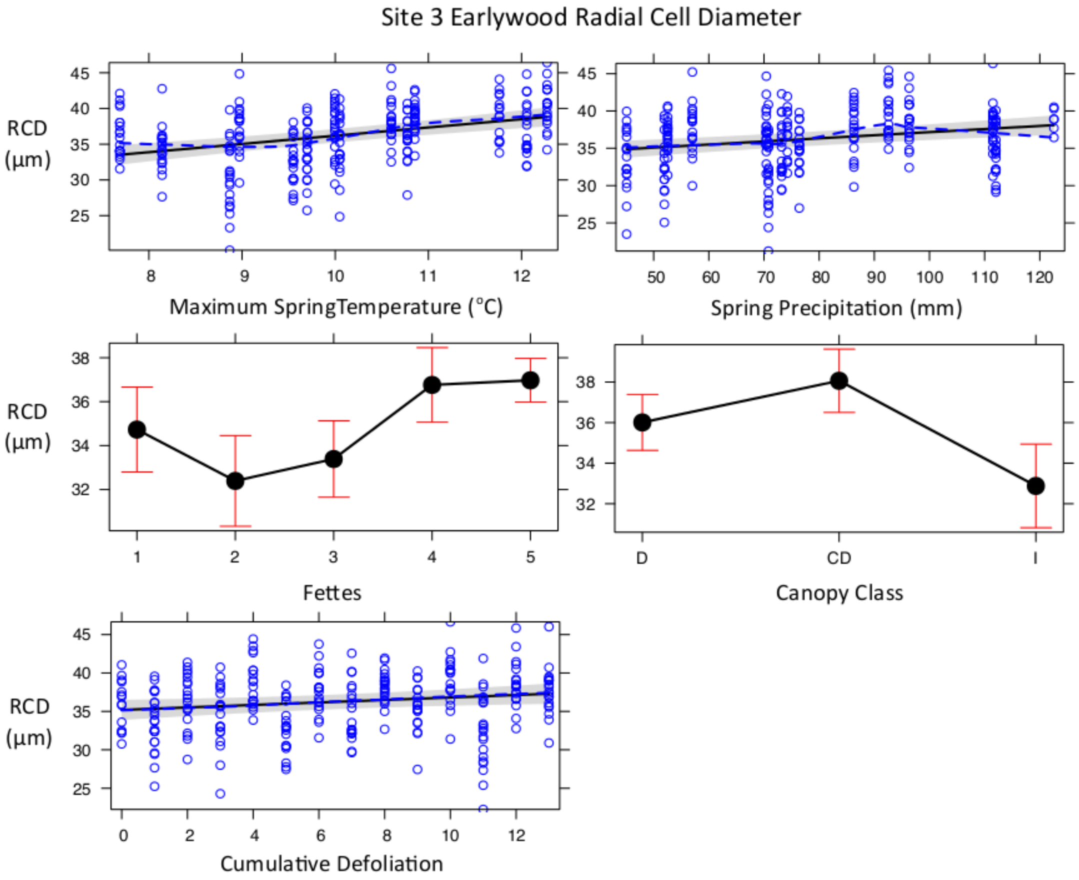


Figure 5.11 Site 3 earlywood radial cell diameter with partial-residuals plotted on the scale of the original anatomical parameter on the vertical axis. Individual plots are arranged by highest *F* statistic and include only significant predictors (Table 5.4). The black solid line is the regression (same slope as the original model), they grey shading represents the 95% point-wise confidence limits for the conditional mean response, the dashed blue line is flexible locally weighted regression that shows whether the data are nonlinear, and the error bars on the categorical variables are the standard error of the estimate.

significant. Latewood radial cell diameter was most strongly predicted by June precipitation, followed by spring precipitation, cumulative defoliation and defoliation severity (Table 5.4). Positive trends existed between latewood cell size and June and spring precipitation, but was weak with spring precipitation, and a negative trend was evident between latewood cell size and cumulative defoliation (Fig. 5.13). Pairwise comparisons of defoliation severity (Fettes) indicated that means were significantly

($p<0.05$) different between 3-5 (Fig. 5.13). Percent latewood was explained by July precipitation and June precipitation, however, this relationship was weak (Table 5.4); positive trends existed with July and June precipitation, and the locally weighted regression illustrates that this anatomical parameter displays the most nonlinearity (Fig. 5.14) compared to the other earlywood and latewood variables.

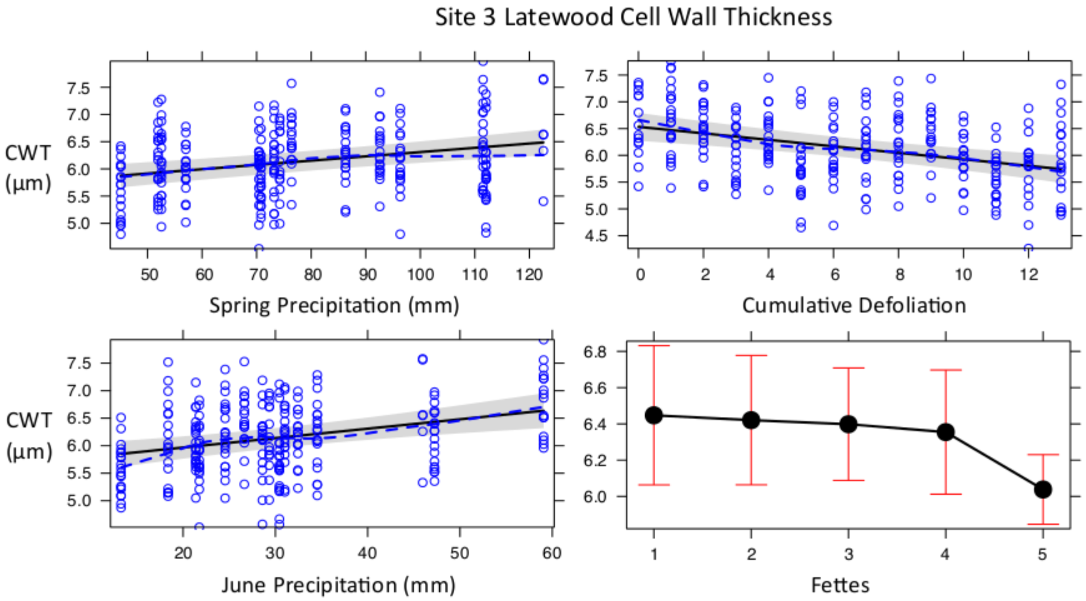


Figure 5.12 Site 3 latewood cell wall thickness with partial-residuals plotted on the scale of the original anatomical parameter on the vertical axis. Individual plots are arranged by highest *F* statistic and include only significant predictors (Table 5.4). The black solid line is the regression (same slope as the original model), they grey shading represents the 95% point-wise confidence limits for the conditional mean response, the dashed blue line is flexible locally weighted regression that shows whether the data are nonlinear, and the error bars on the categorical variables are the standard error of the estimate.

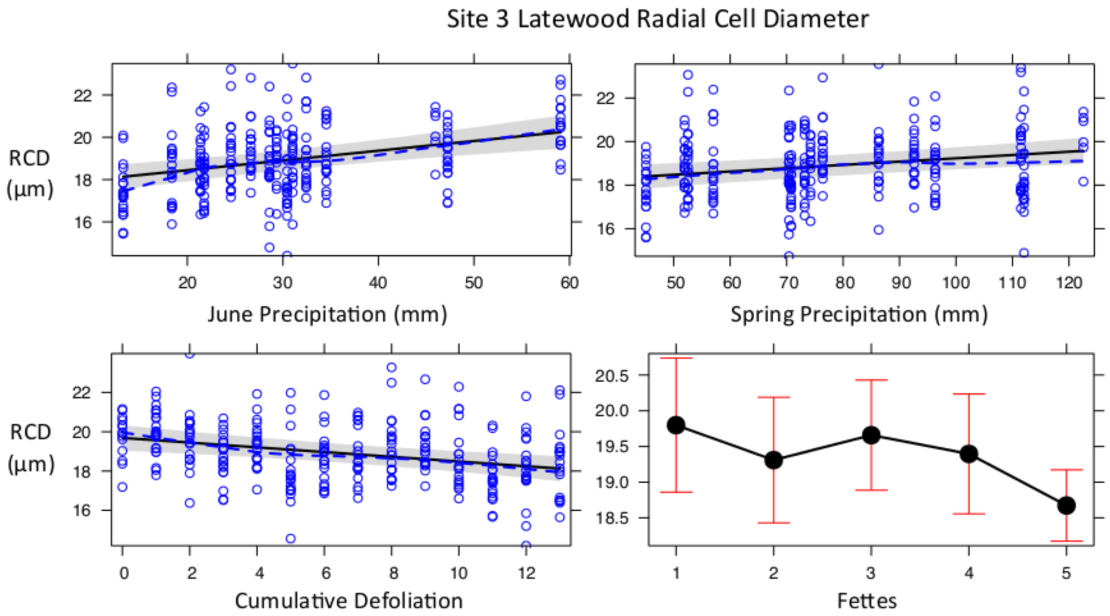


Figure 5.13 Site 3 radial cell diameter partial-residuals plotted on the scale of the original anatomical parameter on the vertical axis. Individual plots are arranged by highest *F* statistic and include only significant predictors (Table 5.4). The black solid line is the regression (same slope as the original model), they grey shading represents the 95% point-wise confidence limits for the conditional mean response, the dashed blue line is flexible locally weighted regression that shows whether the data are nonlinear.

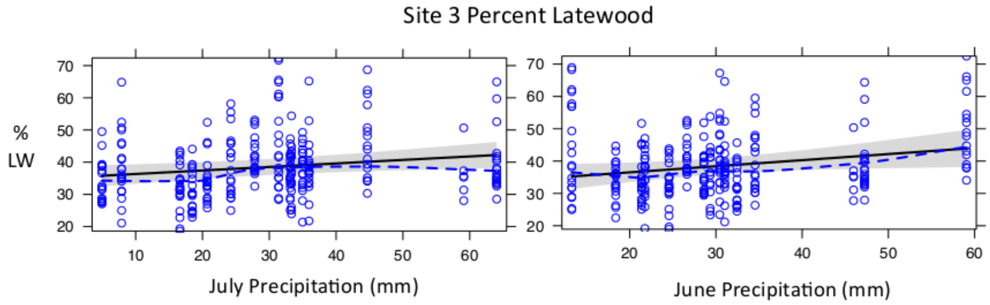


Figure 5.14 Site 3 percent latewood with partial-residuals plotted on the scale of the original anatomical parameter on the vertical axis. Individual plots are arranged by highest *F* statistic and include only significant predictors (Table 5.4). The black solid line is the regression (same slope as the original model), they grey shading represents the 95% point-wise confidence limits for the conditional mean response, the dashed blue line is flexible locally weighted regression that shows whether the data are nonlinear.

At Site 4, earlywood lumen area was predicted by canopy class and defoliation severity (Table 5.5). Pairwise comparisons of the means revealed that D-I and CD-I trees were significantly ($p<0.01$) different from one another; however, there were no significant differences in defoliation severity (Fettes) (Fig. 5.15). Earlywood radial cell diameter was predicted by canopy class and defoliation severity (Table 5.5). Pairwise comparisons indicated defoliation severity (Fettes) 1-2, 2-5, and 3-5 were significantly ($p<0.05$) different from one another; canopy class D-I and CD-I canopy classes were significantly ($p<0.01$) different from one another (Fig. 5.16).

At Site 4, latewood lumen area was not significantly associated with any of the predictor variables (Table 5.5). Latewood cell wall thickness was best predicted by June precipitation, maximum spring temperature, July precipitation, and defoliation severity (Table 5.5); there were positive trends between latewood cell wall thickness and June precipitation, and maximum spring temperature, and a negative trend between latewood cell wall thickness and July precipitation (Fig. 5.17). Pairwise comparisons indicated that the means were significantly ($p<0.05$) different for defoliation severity (Fettes): 1-2, 2-3, 2-4, 2-5, and 3-4 (Fig. 5.17). Latewood radial cell diameter was best predicted by June precipitation, maximum spring temperature, defoliation severity, spring precipitation, and canopy class (Table 5.5). Partial-residual plots showed latewood cell size had positive trends with the significant climatic variables, which were strongest with June precipitation (Fig. 5.18). Pairwise comparisons indicated that the means were significantly ($p<0.05$) different for defoliation severity (Fettes) including: 1-2, 2-3, 2-4 and 2-5; canopy class means between D-I latewood cell sizes were significantly ($p<0.01$) different (Fig. 5.18). Percent latewood at Site 4 was predicted by maximum spring temperature and spring precipitation (Table 5.5); trends were weakly positive, especially between percent latewood and spring precipitation (Fig. 5.19).

Table 5.5 ANOVA results for Site 4, showing influence of model fixed effects on anatomical parameters in Douglas-fir forests of southern interior, British Columbia. Text in bold refers to significance effects ($p<0.05$).

Factor	Degrees of Freedom		Percent Latewood		Lumen area		Cell wall thickness		Radial cell diameter	
	Num	Den	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Earlywood										
CC	2	17	-	-	9.33	**0.002**	1.31	0.295	10.23	**<0.0001**
FET	4	250	-	-	4.74	**0.001**	2.35	0.055	12.94	**0.001**
CUM	1	250	-	-	1.53	0.217	0.00	0.976	0.03	0.853
MT_SP	1	250	-	-	0.27	0.605	0.05	0.821	0.07	0.789
P_SP	1	250	-	-	1.19	0.276	0.29	0.588	1.90	0.169
P_JUN	1	250	-	-	2.87	0.091	0.03	0.851	2.53	0.113
P_JUL	1	250	-	-	0.98	0.322	0.00	0.958	0.00	0.924
Latewood										
CC	2	17	1.46	0.259	2.51	0.111	2.29	0.131	4.56	**0.027**
FET	4	250	1.69	0.153	0.28	0.891	5.27	**<0.0001**	6.47	**0.001**
CUM	1	250	0.51	0.475	0.01	0.910	0.30	0.585	0.02	0.896
MT_SP	1	250	17.64	**<0.0001**	0.56	0.453	19.14	**<0.0001**	10.72	**0.001**
P_SP	1	250	4.48	**0.035**	1.67	0.196	9.05	**0.003**	5.19	**0.023**
P_JUN	1	250	0.56	0.452	0.09	0.757	29.76	**<0.0001**	29.83	**<0.0001**
P_JUL	1	250	5.11	0.736	0.22	0.641	7.36	**0.007**	2.51	0.114

Abbreviations: Num = numerator; Den = denominator; CC = canopy class; FET = defoliation severity (Fettes); CUM = cumulative defoliation; MT_SP = maximum spring temperature; P_SP = spring precipitation; P_JUN = June precipitation; P_JUL = July precipitation (Table 5.3).

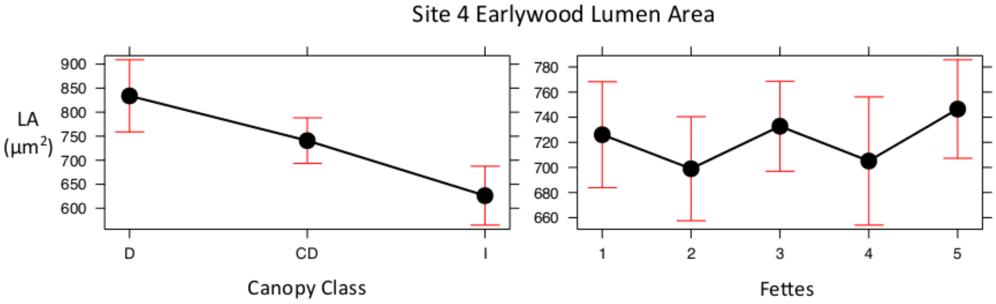


Figure 5.15 Site 4 earlywood lumen area with partial-residuals plotted on the scale of the original anatomical parameter on the vertical axis. Individual plots are arranged by highest *F* statistic and include only significant predictors (Table 5.5). The error bars on the categorical variables are the standard error of the estimate.

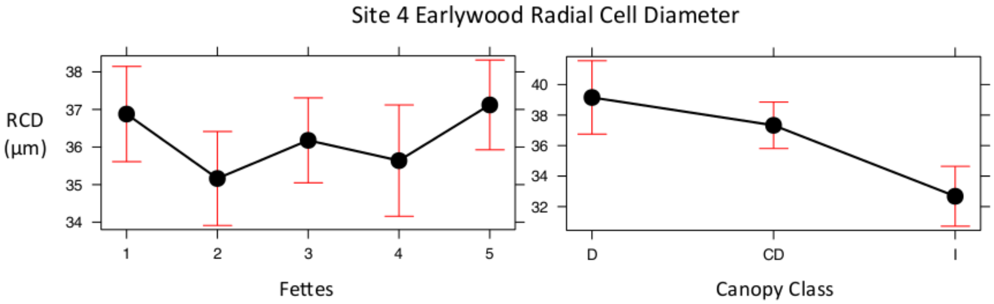


Figure 5.16 Site 4 earlywood radial cell diameter with partial-residuals plotted on the scale of the original anatomical parameter on the vertical axis. Individual plots are arranged by highest *F* statistic and include only significant predictors (Table 5.5). The error bars on the categorical variables are the standard error of the estimate.

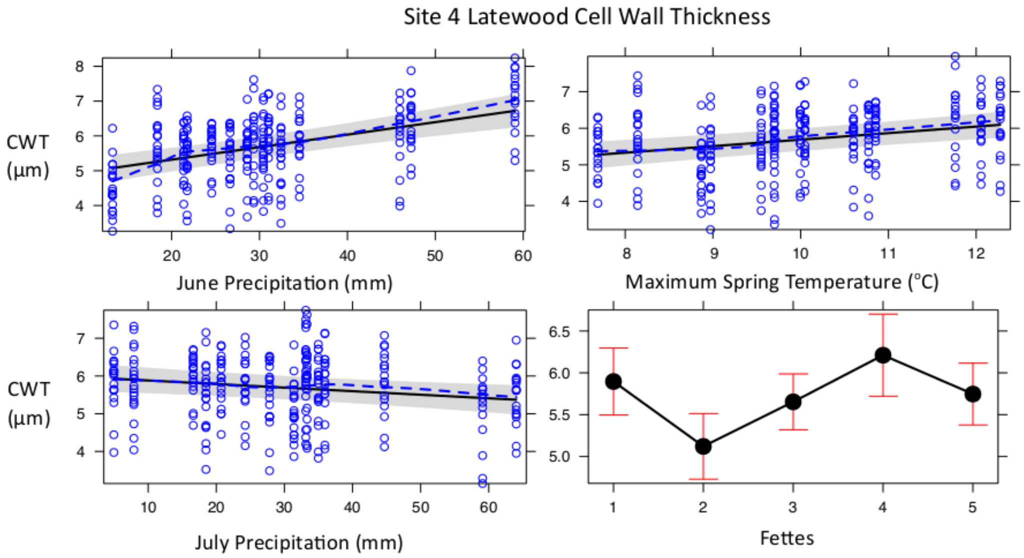


Figure 5.17 Site 4 latewood cell wall thickness with partial-residuals plotted on the scale of the original anatomical parameter on the vertical axis. Individual plots are arranged by highest *F* statistic and include only significant predictors (Table 5.5). The black solid line is the regression (same slope as the original model), they grey shading represents the 95% point-wise confidence limits for the conditional mean response, the dashed blue line is flexible locally weighted regression that shows whether the data are nonlinear, and the error bars on the categorical variables are the standard error of the estimate.

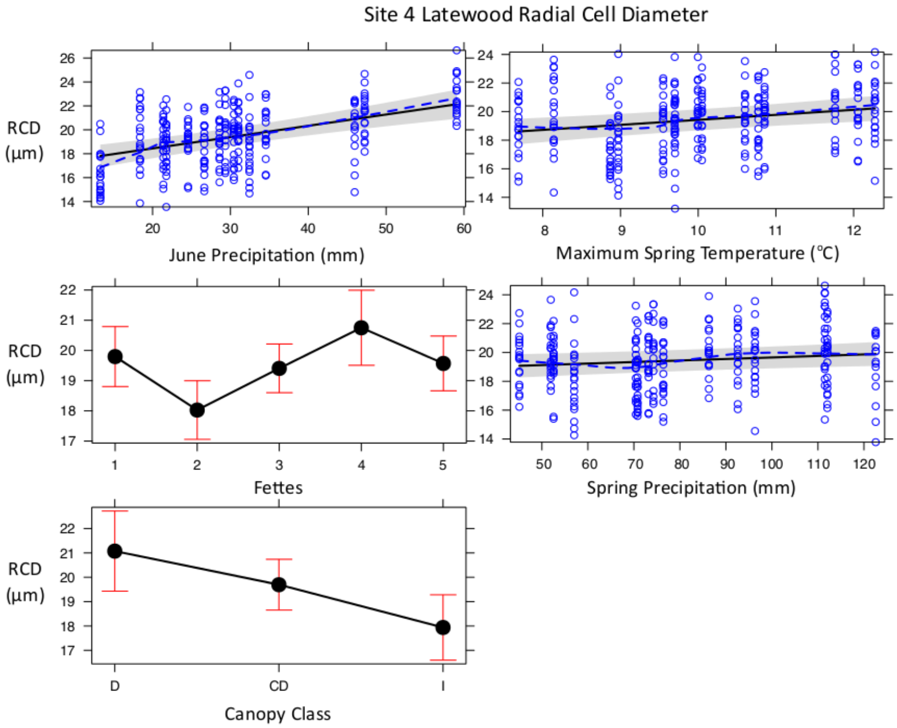


Figure 5.18 Site 4 latewood radial cell diameter with partial-residuals plotted on the scale of the original anatomical parameter on the vertical axis. Individual plots are arranged by highest *F* statistic and include only significant predictors (Table 5.5). The black solid line is the regression (same slope as the original model), they grey shading represents the 95% point-wise confidence limits for the conditional mean response, the dashed blue line is flexible locally weighted regression that shows whether the data are nonlinear, and the error bars on the categorical variables are the standard error of the estimate.

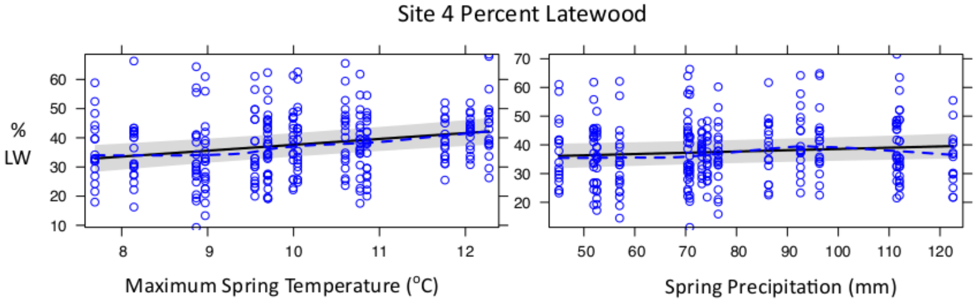


Figure 5.19 Site 4 percent latewood with partial-residuals plotted on the scale of the original anatomical parameter on the vertical axis. Individual plots are arranged by highest *F* statistic and include only significant predictors (Table 5.5). The black solid line is the regression (same slope as the original model), they grey shading represents the 95% point-wise confidence limits for the conditional mean response, the dashed blue line is flexible locally weighted regression that shows whether the data are nonlinear.

5.8 Discussion

Our results confirm that growing season climatic variability, canopy class and WSB outbreak severity and duration affect wood anatomical characteristics in the stemwood of interior Douglas-fir (Tables 5.4 and 5.5; Figs. 5.10 to 5.19). Earlywood lumen area, earlywood radial cell diameter, latewood cell wall thickness, latewood radial cell diameter, and percent latewood (collectively referred to as sensitive anatomical variables) were associated with a number of the predictors in the linear mixed effects models (Tables 5.4 and 5.5). Earlywood cell wall thickness and latewood lumen area were not associated with the predictor variables (Tables 5.4 and 5.5), and the complacency of these variables (Figs. 5.7 and 5.8) is consistent with other studies on the influence of insect herbivory on stemwood anatomical characteristics (Liang et al. 1997, Axelson et al. 2014). Earlywood lumen area and earlywood cell size increased from 1997 to 2011 (Fig. 5.7), while latewood cell wall thickness, latewood cell size and percent latewood decreased from 1997 to 2011 (Figs. 5.8 to 5.9). The positive (earlywood) or negative (latewood) trends were especially pronounced at Site 3, whereas at Site 4 the visual differences between canopy classes were distinct (Figs. 5.7 to 5.9).

Climatically, the stands in the study area were located in xeric-hot (Site 3) or dry-cool (Site 4) biogeoclimatic subzones, where growing season moisture deficits are common (Figs. 5.2 and 5.6) (Lloyd et al. 1990). June precipitation, spring maximum temperature and spring precipitation were strong predictors of various anatomical variables at each site (Tables 5.4 and 5.5). Cambial reactivation is regulated by internal factors, such as plant hormones (e.g., auxin) (Larson 1962), and environmental factors, such as temperature, rainfall and photoperiod (Brix and Mitchell 1980, Begum et al. 2013). The association of maximum spring temperature and spring precipitation with earlywood variables at Site 3 suggests that March – May period is related to cambial reactivation at this site. At Site 4, the predominance of these relationships with latewood variables suggests that cambial reactivation is delayed at this higher elevation and cooler-wetter site. Differences in temperature between sites has been demonstrated to offset the timing of xylem formation in the eastern boreal stands in Quebec, Canada (Deslauriers et al. 2003) and in Douglas-fir stands in the Pacific Northwest (Grotta et al. 2005).

May and June are the two wettest growing season months (Fig. 5.2), and June precipitation was associated with increases in latewood cell wall thickness and latewood radial cell diameter at both sites (Figs. 5.12 to 5.13 and 5.17 to 5.18; Tables 5.4 and 5.5), which is consistent with the correlation analysis between June precipitation and standardized tree-ring chronologies (Fig. 5.5). Curiously, increases in July precipitation were associated with negative trends in latewood cell wall thickness at Site 4 (Fig. 5.17), which was not consistent with correlations between this climate variable and the standardized tree-ring chronology (Fig. 5.5). If this relationship has any biological meaning, we can only speculate that increasing July precipitation is accompanied by cooler conditions that are not conducive to cell wall thickening. However, if this was the case we would expect to see similar negative trends between July precipitation and latewood radial cell diameter (Fig. 5.18), as at Site 3 there is coherence between significant predictors for both latewood cell wall thickness and latewood cell size (Figs. 5. 12 and 5.13).

In the temperate zone the highest period of cell production occurs in June (Rossi et al. 2006), when precipitation plays an important role in xylem development and maturation by supplying water to the crown and by transporting carbohydrates and auxin to the cambium (Kramer 1964, Zahner 1968). Wood anatomical variables can be more sensitive to monthly climate variables than either ring-width or density chronologies, such as average lumen area July to September precipitation at high latitude sites in Sweden (Pritzkow et al. 2014). In the Great Basin of the western U.S., spring temperature was highly correlated with earlywood anatomical features such as lumen area and cell diameter, while latewood features were correlated to summer precipitation and temperature variables (Ziaco et al. 2014). Similarly in our study, more nuanced relationships between anatomical and climatic variables were revealed in the mixed effects modeling, than by the correlation analysis using tree-ring chronologies (Fig. 5.5).

Competitive effects in struturally complex stands was a significant predictor of earlywood lumen area and earlywood cell size at both sites (Tables 5.4 and 5.5). Partial-residual plots revealed the negative association between earlywood lumen area and earlywood cell size with canopy class (Fig. 5.10 to 5.11 and Fig. 5.15 to 5.16); I trees had the smallest values, and post-hoc testing indicated that means were significantly different between D-I and CD-I layers primarily. It is well known that juvenile wood is characterized by progressive changes in cell features and wood properties (Panshin and deZeeuw 1980). In Douglas-fir, mature wood characteristics are present at an average age of 26 years (range 15-38 years) (Abdel-Gadir and Krahmer 1993). In our study, trees in the I canopy class averaged 75 years old at both sites with the youngest trees ranging between 52 and 66 years (Table 5.3). Therefore the relationships between canopy class and anatomical earlywood characteristics are related to competitive effects and not instable wood properties of juvenile growth. Earlywood lumen area and cell size were the smallest for intermediate trees over the 15-year measurement period (Figs. 5.7), which was especially pronounced at Site 4 (Figs. 5.7 and 5.15-5.16; Table 5.5). We suggest that the effect of competition at Site 4 were related to stand density, which averaged around 700 trees/hectare. Trees with larger more vigorous crowns have been found to have higher auxin availability, which increases cambial production (Larson 1962), whereas cambial production in suppressed trees may be inhibited due to auxin deficiency associated with their smaller crowns (Kozlowski and Peterson 1962, Larson 1962). Competitive stress resulting from soil water deficits, which would be expected to occur at sites with higher tree density or at open sites with greater amounts of soil evaporation, the principal determinate of water use at both the tree- and stand-level is leaf area. In xeric Douglas-fir forests, water use by the smallest trees accounts for 21% to 42% of the average daily stand water use, while large trees (> 20 cm DBH) use an estimated 44% to 75% of soil moisture (Simpson 2000). Intermediate trees not only have a competitive disadvantage due to their position and smaller crowns, but also tend to be more severely defoliated by WSB then canopy D and CDs (Maclauchlan and Brooks 2009). This may explain why earlywood values in the I canopy class at Site 3 were fairly similar to the D and CD trees in 1997-98 (Fig. 5.7) as the site has lower tree density and therefore lower competitive effects than Site 4, and WSB defoliation (Fig. 5.3) and radial growth declines (Fig. 5.4) were just beginning.

Defoliation severity and cumulative defoliation played different roles for earlywood and latewood variables at each site (Tables 5.4 and 5.5). At Site 3, defoliation severity was the strongest predictor of earlywood lumen area and radial cell diameter (Fig. 5.7; Table 5.4), while cumulative defoliation was a stronger predictor for latewood variables (Fig. 5.8; Table 5.4). At Site 4 defoliation severity was a significant predictor of earlywood lumen area and earlywood cell size, latewood cell wall thickness and latewood cell size, while cumulative defoliation had no influence (Table 5.5). We suggest that these differences arise from the variations in defoliation severity and duration at each site (Fig. 5.3).

For trends in earlywood variables, particularly as Site 3, crown development and condition influences tracheid radial diameter, which is under hormonal control (Devine and Harrington 2009). Cambial reactivation precedes bud burst by a number of weeks in Douglas-fir (Brix and Mitchell 1980, Li and Adams 1994) in a feedback loop that involves mobilization of growth hormones (Larson 1962, Uggla et al. 2001) from physiologically active vegetative buds (Owens 1969). Earlywood tracheid development and enlargement occurs quickly (Deslauriers et al. 2003) and in coastal Douglas-fir starts anywhere from mid-April (Li and Adams 1994) to mid-May (Grotta et al. 2005). With sustained defoliation periods, often of high severity, acute and progressive reductions in crown biomass result from consecutive years of defoliation (Piene and MacLean 1999). As crown volume decreases due to cumulative foliage loss, trees are deprived of a full suite of photosynthetically active foliage, limiting production of carbohydrates (glucose, fructose and sucrose), starch and lipids, and also compromising the role the crown plays as a photosynthate sink early in the growing season (Devine and Harrington 2009).

At our study sites, we suspect that earlywood development starts in mid- to late May, when WSB larvae are still small and not yet consuming large amounts of new growth. Increases in earlywood lumen area and earlywood radial cell diameter would occur during a WSB outbreak in order to enhance transport of growth hormones down the stem to the cambium, not to enhance water transport to the crown as reduced crown volume decreases the transpiring surface, which in turn improves water status (Ericsson and Hellkvist 1980). As crown condition is depleted through severe defoliation, especially when cumulative in nature (Fig. 5.3), conducting capacity needs to be enhanced in the earlywood tracheids (Fig. 5.7), which can occur from even small increases in tracheid diameter (Sperry et al. 2006). Another effect of sustained and severe defoliation is that partial to full removal of buds by WSB could trigger a compensatory increase in the remaining buds, differentiation of suppressed lateral buds (Piene and MacLean 1999), and/or epicormic branching to replace dead and dying crown components (Bryan and Lanner 1981). These coping mechanisms may in turn increase utilization of starch to offset decreased photosynthate production (Ericcson and Hellkvist 1980).

Latewood cell wall thickness and radial cell diameter decreased over the 15-year period at Site 3, and oscillated with short-term decreases at Site 4 (Fig. 5.8). The intensive feeding pressure, both severe (>75%) and cumulative at Site 3 (Fig. 5.3), corresponded with negative trends in latewood cell wall thickness and latewood cell size

(Fig. 5.8) and strongly negative associations between these parameters and cumulative defoliation (Figs. 5.12 to 5.13). At Site 4, cumulative defoliation played a less important role as a predictor overall (Table 5.5), which is consistent the less cumulative nature of the defoliation at this site (Fig. 5.3). In latewood tracheids cell wall thickening becomes the main sink for photosynthates produced by current-year foliage (Larson 1994). Axelson et al. (2014) found that maximum reductions in latewood characteristics were associated with sustained and severe periods of budworm feeding, when cumulative loss of current-year foliage resulted in gradually consumed and depleted carbohydrate reserves (Reich et al. 1993). Similarly, in this study, latewood tracheid development and maturation is underway by mid-July (Grotta et al. 2005), after the WSB has maximally defoliated the current years foliage; decreased production of photosynthates reduces latewood cell wall thickness and radial cell diameter (Fig. 5.8). This causal effect is evident with the onset of defoliation in 1997-98, which had not yet been prolonged or severe at either site (Fig. 5.3). Latewood cell wall thickness and latewood cell size had the highest values over the measurement window, particularly at Site 3 (Fig. 5.8), and at Site 4, decreases in latewood tracheid values appear to 'recover' around 2004 to 2006 following a period of no or low defoliation (Figs. 5.3 and 5.8). In a study of needle abscission from Swiss needle cast (*Phaeocryptopus gaeumannii* (Rohde) Petrak), Saffell et al. (2014) found that non-structural carbon retention was greater in the crown versus the trunk; the presence of the disease forced trees to sacrifice stem growth and stem non-structural carbon storage in order to maintain crown growth. We suggest a similar mechanism is operating in our study as stem growth is severely reduced by WSB feeding (Fig. 5.4) and latewood tracheid variables progressively decreased with increasing cumulative defoliation, or slightly recovered when feeding severity and duration eased (Figs. 5.4 and 5.8).

Percent latewood is considered the main driver of wood density (Zobel and Van Buijtenen 1989), decreases in cell wall thickness and percent of latewood result in lower wood density (Wimmer 1995, Rathgeber et al. 2006). In our study, percent latewood had decreasing trends during the 15-year measurement period at Site 3, and at Site 4 oscillated over time similar to the other latewood variables at this site (Figs. 5.8 and 5.9). Grotta et al. (2005) found that percent latewood and ring width were negatively correlated, indicating that slower-growing trees produced more latewood relative to earlywood. Similarly in trees infected with Swiss needle cast, narrow tree rings corresponded to higher percent latewood (Johnson et al. 2005). Alternatively, in southwestern B.C. Axelson et al. (2014) found that low percent latewood values corresponded to low radial increment resulting from WSB defoliation. Similarly, Douglas-fir trees exposed to air pollution that had the greatest needle loss also had the lowest percent latewood and lowest radial growth (de Kort et al. 1991, de Kort 1993). During larch sawfly (*Pristiphora erichsonii* (Hartig)) defoliation of eastern larch (*Larix laricina* (Du Roi) K. Koch) rings with thin latewood cell walls and reduced percent latewood were formed during an outbreak (Liang et al. 1997). In the current study when cumulative WSB defoliation and severity were the greatest, the strongest declines of annual radial increment (Fig. 5.4) and sustained decreases in percent latewood occurred (Fig. 5.9).

Douglas-fir is more resistant to drought-induced cavitation than ponderosa pine (Piñol and Sala 2000), which may be related to the role that latewood tracheids play in water storage (Domec and Gartner 2002). Trees with higher wood density, thicker latewood cell walls and smaller lumen diameters are expected to be more resistant to drought (Martinez-Meier et al. 2008, Dalla-Salda et al. 2009). In defoliated Scots pine (*Pinus sylvestris* L.) there is enhanced sensitivity to drought as trees lack compensatory increases in needle photosynthetic capacity resulting in greater reductions of non-structural carbon relative to non-defoliated trees (Poyatos et al. 2013). On the other hand, defoliation has been found to induce compensatory factors such as epicormic branching, increased photosynthetic rate (Reich et al. 1993), altered allocation of carbohydrates that favours foliage production over stem growth (Ericsson and Hellkvist 1980), and greater non-structural carbon retention in the crown versus the trunk (Saffell et al. 2014). The transition from earlywood to latewood formation is related to declines in summer soil water availability (Kennedy 1961, Brix 1972, Robertson et al. 1990). The xeric nature of

Douglas-fir stands in the study area, especially at Site 3, could be expected to account for significant soil moisture deficits during the growing season. Soil moisture would be further depleted by the total water used by the stand (i.e., productivity), and the relative amount used by individuals (i.e., competition) (Simpson 2000), as well as water use by competing vegetation such as pinegrass. Given the role that latewood properties play in the drought tolerance of Douglas-fir (Domec and Gartner 2002, Martinez-Meier et al. 2008, Dalla-Salda et al. 2009, Dalla-Salda et al. 2011) may explain why decreases in percent latewood were not associated with WSB defoliation at either site (Tables 5.4 and 5.5). While lower cell wall thickness and lower percent latewood are known to decrease wood density (Wimmer 1995, Rathgeber et al. 2006), it is unclear whether sustained decreases in these latewood variables will make Douglas-fir more susceptible to drought despite its resistence to xylem cavitation (Piñol and Sala 2000).

5.9 Conclusion

This study illustrates how the combined action of climatic variability, sustained and largely severe WSB defoliation, and canopy class affect anatomical characteristics, particularly increases in earlywood lumen area and earlywood cell size and decreases in latewood cell wall thickness and latewood cell size. We used a linear mixed effects modeling approach to overcome analytical challenges arising from our hierarchical, unbalanced and autocorrelated anatomical datasets, and demonstrated that maximum spring (March – May) temperature and canopy class were important predictors of earlywood lumen area and earlywood cell size. June precipitation, cumulative defoliation and defoliation severity were important predictors of latewood cell wall thickness, and latewood cell size. Cumulative defoliation was strongly associated with latewood variables at Site 3, and overall this site had more obvious positive (earlywood) or negative (latewood) trends in anatomical characteristics. We suggest that cumulative defoliation and defoliation severity in combination are important outbreak characteristics that result on measureable impacts to anatomical variables. Declines of key latewood properties, namely cell wall thickness and percent latewood could increase Douglas-fir susceptibility to drought impacts such as morality. Future research could examine a wider range of climatic variables, including soil moisture measurements, relative humidity and growing degree-days to develop a more comprehensive understanding of how climate affect anatomical characteristics; and whether sustained and severe WSB outbreaks trigger irreversible anatomical modifications that contribute to failed drought tolerance in Douglas-fir. In our study the WSB outbreak was ongoing and in its 16th year, so whether anatomical variables continued to increase (earlywood), decline (latewood), or eventually recovered to pre-outbreak levels remains unanswered.

Chapter 6 Conclusion

6.1 Western spruce budworm, management and resilience

WSB disturbances leave ecological signatures at various scales. At the landscape scale, management activities (e.g., fire suppression and harvesting practices) have created a mosaic of densely stocked nearly pure Douglas-fir stands that WSB has exploited through sustained and often locally severe outbreaks. In the B.C. interior, the last 20 years have been dominated by chronic WSB outbreaks that likely result from landscape conditions that are highly suitable and susceptible to WSB epidemics. In the forestry context, where planning horizons vary from annual to multiple decades, these sustained outbreaks can have serious impacts on timber quality and quantity. Timber supply analyses make only coarse adjustments for disturbances, which may not capture how repeated periods of suppressed growth (amongst other impacts) from WSB defoliation negatively impacts merchantable volume. For forest managers, the highly likely mismatch between perceived and actual timber quantity on the landscape will no doubt come as an unpleasant surprise.

At the stand level, WSB affects the composition and structure of affected stands. Compositionally, Douglas-fir produces a sporadic cone crop, which can be further exasperated by budworm feeding on developing reproductive buds and cones resulting in regeneration failures across large components of the landscape. At a structural level budworm damage is the greatest in the understory where suppressed and intermediate trees already suffer from reduced crown biomass due to competition effects in uneven aged stands. While budworm has been thought of as a thinning agent it does not always result in mortality of understory trees, rather outbreaks leave behind densely spaced understory trees with even lower crown biomass and poor vigour, that persist in the understory for decades. These suppressed understory trees act as competitors for very limited soil moisture in xeric stands and continue, despite their depleted crown biomass, to be susceptible to ongoing budworm defoliation, as well as other disturbance agents such as snowpress.

At the tree level, a variety of processes occur during sustained and/or severe defoliation periods resulting in radial increment and volume loss, dieback, and in worst cases mortality. Dieback (i.e., topkill) commonly occurs in suppressed and intermediate individuals, which has major impacts on post-budworm growth recovery and from a forestry perspective substantial negative impact on the wood quality. From a wood quality perspective, the impacts of WSB defoliation cascade to the fundamental building blocks of wood xylem, by modifying cellular structure in ways that not only changes wood quality features (e.g., wood density) but potentially increase the vulnerability of trees to other disturbances such as drought induced mortality.

At long temporal scales, tree ring reconstructions of WSB outbreak dynamics are based on the preferential sampling of old trees that have survived repeated cycles of defoliation. Thus, WSB outbreaks can be thought to be less disturbing to the forest than outbreaks of the spruce budworm in eastern spruce–fir forests that can result in widespread mortality of mature individuals (Pothier and Mailly 2006, Sainte-Marie et al. 2015). This regional distinction demonstrates that not all defoliator population cycles translate into catastrophic forest disturbances (Cooke et al. 2007). In fact, the WSB and the Douglas-fir ecosystem appear to represent a resilient system, with centuries of evidence suggesting the existence of a stable forest-budworm disturbance regime (Swetnam and Lynch 1993). Long-lived species and individuals play an extremely important roles in ecosystem resilience because their persistence indicates they are adapted to the natural disturbance regime, and reduces the potential for invasion of new species that could lead to a threshold change within the ecosystem (Chapin et al. 2004).

Several studies have suggested that changes in WSB outbreak behaviour over the 20th century, i.e., increases in severity (Hadley and Veblen 1993) or synchrony (Hadley and Veblen 1993, Swetnam and Lynch 1993, Campbell et al. 2006), may result from forest management activities during the 19th and 20th centuries, such as fire suppression and selective cutting, which resulted in mixed conifer stands that are more susceptible to WSB outbreaks (Fellin and Dewey 1982, Anderson et al. 1987, Hadley and Veblen 1993, Swetnam and Lynch 1993). Maclauchlan and Brooks (2009) found that multi-layered and selectively harvested stands throughout B.C. supported high budworm populations with elevated levels of defoliation, particularly in the understory layers followed by mortality with intensive WSB defoliation; in young, thinned stands and stands that had never been harvested impacts from budworm defoliation were the least severe. This observation suggests that changes to stand structure through harvesting have influenced the susceptibility of Douglas-fir forests to WSB (Maclauchlan and Brooks 2009) and that silviculture can be used as a management tool to reduce damage.

The influence of forest management activities on insect outbreaks can be direct, such as the time sensitive removal of trees infested with bark beetles, or indirect, such as occurs by modifying stand structure to reduce susceptibility and increase resistance to catastrophic bark beetle attack (Temperli et al. 2014). In B.C., Douglas-fir forest management activities are focused on direct control with the widespread application of the biological insecticide *Bacillus thuringiensis* var. *kurstaki.* This treatment, which is optimally applied when WSB larvae are in 4th instar and consuming larger quantaties of foliage, aims to maximize insect mortality while minimizing the damage done by the WSB in the current year. This approach to WSB management is efficacious in terms of the budworm mortality achieved in treated areas, and is time and cost effective, averaging $30/hectare (Westfall and Ebata 2012-2014). However, this direct control method fails to reduce stand suseptibility, enhance resistance or improve the resilience of Douglas-fir ecosystems. Instead, direct control only temporarily suppresses budworm populations in specific locations at discrete points in time, with WSB populations expanding in different areas in subsequent years. Based on the conclusions reached by Maclauchlan and Brooks (2009) after their extensive analysis of WSB dynamics, indirect control measures oftentimes make stands less susceptible to WSB outbreaks and by removing trees with very poor growth form and vigour ensure that the remaining trees have the growing space and limited moisture resources they need to thrive.

If ecosystem resilience is undermined, it is difficult to predict whether threshold changes will occur, and what future directions an ecosystem will follow (Chapin et al. 2004). A lack of resilience is obvious *a posteriori* when a forest has been significantly altered by stress or disturbance, while *a priori* presence of resilience is much more difficult to quantify (Kolb et al. 1994). This is a fundamental dilemma from a management perspective, as forest managers have fewer financial and human resources to develop long-term strategies that enable forest ecosystems to withstand disturbances and continue to provide ecosystem services.

A major challenge for forest managers will be developing and having in place sound management policies to address the ‘unknowns’ within the complex B.C.’s complex Douglas-fir forests (i.e. Fettig et al. 2013). In the present-day context, the short- and long-term impact of ongoing climate change on Douglas-fir ecosystem processes and disturbance regimes remains poorly understood. Phenology of herbivores is in many cases temperature dependent, and climate change is highly likely to lead to changes in phenology; as temperatures increase the phenology of both the insect herbivore and its host plant is expected to advance (van Asch and Visser 2007). For example, in the WSB system BioSIM 10 projections indicate that significant changes in seasonality have occurred from 1951 to 2012, with just over 1 week advance in phenology (Nealis and Régnière 2013). However, changes in phenology of the insect herbivore and its host will not necessarily change at the same rate. Thomson and Benton (2007) suggested that warming ocean temperatures resulted in accelerated WSB phenology that was not matched by earlier Douglas-fir bud burst in the study region. The influence of climate change will also influence the interactions between species, where small effects on phenology could lead to larger impacts in synchrony and disruptions to trophic interactions (van Asch and Visser 2007). A decrease in ecosystem resistance and resilience to disturbance resulting from increased precariousness due to climate change could result in rapid irreversible changes in long established disturbance-recovery regimes (Chapin et al. 2004).

Forest ecosystems are complex systems made up of many parts (e.g. trees, mammals, birds, insects, etc.) and processes (e.g., mortality, regeneration, disturbance regimes, nutrient cycling, etc.) that interact with one another and their environment over multiple spatial and temporal scales. These interactions give rise to heterogeneous forest structures, which may range from strong and direct to weak and diffuse and can be modified by negative or positive feedback loops (Campbell et al. 2009). The adaptive capacity of complex forest ecosystems is the ability of a system to reconfigure itself in the face of disturbance or stresses without significant decreases in critical aspects such as productivity or composition (Gunderson 2000, Carpenter et al. 2001). A system with adaptive capacity will not be destabilized by positive feedback processes, which in turn will not increase precariousness, and decrease resilience. This condition essentially encapsulates the ideal of forest health, which as a management goal needs to incorporate understanding of how disturbance dynamics impact processes and structures within ecosystems, if positive or negative feedbacks are more likely, and if the system has adaptive capacity (Drever et al. 2006, Fischer et al. 2006, Campbell et al. 2009).

This dissertation contributes information on the influence of WSB at multiple temporal and spatial scales. Douglas-fir appears to be inherently adapted to withstand disturbance and has thus far been resilient to multiple, severe and sustained WSB outbreaks in various areas of its range. The Douglas-fir forests, particularly within the interior of B.C., are associated with a landscape highly modified by fire suppression and harvesting practices. It remains to be seen whether these ecosystems can continue to be resilient and recover from disturbances.

6.2 Summary of results

The research in this dissertation is presented in the format of journal articles, and manuscripts in preparation for publication. Here I summarize central findings from the thesis, while more detailed results and discussion can be found in Chapters 3-5.

1. Mixed-conifer stands of long-lived host and non-host trees (for western spruce budworm) are uncommon in central interior forests of B.C. I have demonstrated that reconstructions based on proximal lodgepole pine and distal ponderosa pine chronologies produce consistent reconstructions across the Douglas-fir sites. This finding demonstrates the viability of using more distant non-hosts to reconstruct western spruce budworm outbreaks, which to my knowledge has not been done before. For studies at the northern and eastern range limits of Douglas-fir this is an important finding as co-occurring long-lived non-hosts are even more sparse in this landscape.

2. My reconstruction of western spruce budworm outbreak dynamics over 400 years in central British Columbia does not support the perception that the WSB has been expanding its range northward into the Cariboo Region in recent decades. Rather, over the period of record (1576 to 2011) there were 12 low-intensity outbreaks with an average duration of 15 years and periodicity of ~30 years (return interval) and ~32 years (wavelet).

3. Sensitivity analyses illustrates that defining light, moderate and severe WSB intensity thresholds modifies the number of reconstructed outbreaks, their duration and mean return interval. Sensitivity analyses makes an important contribution towards understanding the nuances of outbreak dynamics, which are known to vary widely in severity even within a single stand, across the landscape.

4. My examination of the anatomical impact of a western spruce budworm outbreak is the first study of its kind in mature Douglas-fir forests. The study revealed that significant modifications, primarily in latewood properties, occurred in response to defoliation at a 2-year lag. The discovery that once the WSB-induced defoliation ceased these properties returned to their pre-outbreak properties demonstrated the inherent plasticity of Douglas-fir trees to defoliation.

5. Previous studies of biotic disturbances on the anatomical properties of wood suggest that the resulting narrow annual rings produce denser wood due to increases in percent latewood. My findings indicate that WSB feeding in fact results in narrow rings with significantly less latewood. The resulting changes in wood density could have significant impacts to wood quality once trees have been harvested and entered the commodity chain.

6. The impact of a 15-year long western spruce budworm outbreak was examined at the anatomical level in uneven-aged mature Douglas-fir forests in the southern interior. I examined how climatic variability, defoliation severity and duration effect wood anatomical properties of both earlywood and latewood tracheids. Increases in cell diameter in the earlywood, and decreases in latewood cell wall thickness and cell diameter during a period of chronic WSB feeding corroborate related findings from the coastal-transition study of even-aged mature Douglas-fir forests described in Chapter 4.

7. My findings reveal that WSB defoliation duration and intensity, as well as site factors that mediate moisture conditions, have a strong influence on the degree to which anatomical properties were effected at each site. This finding suggests that the radial growth of Douglas-fir is very tolerant to environmental stress, competition and disturbance.

6.3 Future research

Answering research questions has the tendency to generate a multitude of new and sometimes unexpected questions. At the conclusion of this thesis I have more questions about Douglas-fir and WSB disturbance interactions than I started with, below is a list of future research topics.

1. Reconstructions of WSB dynamics at the northern and eastern range limits of Douglas-fir will be limited by the existing methodology of requiring a non-host to correct for climatic variability, as long-lived non-hosts can be rare in these environments. Research efforts should focus on developing or applying new statistical methodologies that eliminate the need for a non-host climatic correction to develop robust reconstructions of WSB outbreaks.

2. A comprehensive and collaborative study of WSB outbreak dynamics across the range of Douglas-fir in western North America. A cohesive approach to chronology and reconstruction development, and analysis would shed light on WSB outbreak frequency,

duration, severity, and periodicity, as well as the entraining role of climate on outbreaks across complex geographical areas.

3. This research focused exclusively at quantifying changes in radial growth or cellular characteristics during WSB outbreaks. Studying the recovery of Douglas-fir after WSB defoliation on various canopy cohorts would increase our understanding of the long-term impacts of discrete feeding events; different rates of recovery depending on severity and/or duration of defoliated individuals, and the influence of canopy position on recovery; and whether compensatory growth mechanisms are initiated after all defoliation events or if this depends on other factors such as disturbance interactions or climatic stress.

4. Long-term research installations in differing Douglas-fir forests are required to quantify how silvicultural treatments, such as: thinning from above (overstory removal), thinning from below (understory removal), under planting with mixed species (e.g., birch) in various combinations and intensities impacts WSB outbreak intensity, duration, and host response over multiple outbreak cycles. This research would quantify which management activities will enhance resilience and reduce long-term susceptibility to WSB.

5. From an anatomical perspective there is much that could be done to gain a more comprehensive understanding of the processes and structures that change and interact during WSB defoliation events, including studies that:

    a. Examine intra-annual changes to earlywood and latewood tracheids to determine if there are changes in timing of cambial reactivation, earlywood/latewood formation windows, if there is a foliage loss threshold that occurs within the feeding/tracheid formation season;

    b. Evaluate whether modifications in tracheid structure occur in different portions of the tree (e.g., roots, branches, stemwood located higher in the crown);

    c. Use different slide preparation techniques (e.g., staining) to determine if changes occur in lignification in the latewood tracheids;

    d. Conduct foliage sampling throughout single to multiple defoliation years to determine how carbon balance, storage and utilization patterns change throughout a WSB outbreak period;

    e. Quantify how changes in tracheid properties, such as lower percentages of latewood and thinner latewood cell walls, impact wood quality properties such as density, modus of elasticity and microfibril angle; and,

    f. Include or collect climatological and/or micro climatological measurements such as temperature, relative humidity, precipitation, evaporation and evapotranspiration, and soil moisture content to gain a comprehensive understanding of key climatological variables that control or restrict tree physiological processes during a WSB outbreak.

6. Determine if ecological thresholds exist for Douglas-fir, where the species is no longer able to resist or temporarily modify processes in order to withstand environmental stress. What are the consequences if thresholds are reached or crossed?

References Cited

Abdel-Gadir, Y. A., and R. L. Krahmer. 1993. Estimating the age of demarcation of juvenile and mature wood in Douglas-fir. Wood and Fiber Science 25:242–249.

Agee, J. 1993. Fire Ecology of Pacific Northwest forests. Island Press, Washington, DC.

Alfaro, R., and L. E. Maclauchlan. 1992. A method to calculate the losses caused by western spruce budworm in uneven-aged Douglas-fir forests of British Columbia. Forest Ecology and Management 55:295–313.

Alfaro, R., G. Van Sickle, A. Thomson, and E. Wegwitz. 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. Canadian Journal of Forest Research 12:780–787.

Alfaro, R., A. Thomson, and G. Van Sickle. 1985. Quantification of Douglas-fir growth losess caused by western spruce budworm defoliation using stem analysis. Canadian Journal of Forest Research 15:5–9.

Alfaro, R., R. Campbell, P. Vera, B. Hawkes, and T. Shore. 2004. Dendroecological reconstruction of mountain pine beetle outbreaks in the Chilcotin plateau of British Columbia, In: Mountain pine beetle symposium: challenges and solutions. T. L. Shore, J. E. Brooks, and J. E. Stone (Eds.). Information Report BC-X-399. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC.

Alfaro, R., J. Axelson, K. Lewis, J. Barichivich, L. Duran, H. Gee, L. Haavik, K. Hardy, E. Jones, L. Lopez, C. Mansilla, M. Pena, and L. Suarez. 2008. Dendroecological reconstruction of western spruce budworm (*Choristoneura occidentalis* Freeman) at McCall Lakes, Peachland, British Columbia, Canada. North American Dendroecological Fieldweek. URL: https://sites.google.com/site/northamericandendrofieldweek/2008 [Accessed June 2015].

Alfaro, R., A. Battisti, A. Carroll, R. Fleming, J. Hantula, D. Francis, P. E. Hennon, D. Lanfranco, A. Lilja, M. Müller, M. Ramos, and A. Woods. 2010. Forest health in a changing environment. In: Forests and Society – Responding to Global Drivers of Change. G. Mery, P. Kitila, G. Galloway, R. I. Alfaro, M. Kanninen, M. Lobovikov, and J. Varjo (Eds). IUFRO World Series Vol. 25. International Union of Forest Research Organizations, Vienna, Austria. pp. 113-134.

Alfaro, R. I., J. Berg, and J. Axelson. 2014. Periodicity of western spruce budworm in southern British Columbia, Canada. Forest Ecology and Management 315:72–79.

Alfaro, R.I., L. vanAkker, and B. Hawkes. 2015. Characteristics of forest legacies following two mountain pine beetle outbreaks in British Columbia, Canada. Canadian Journal of Forest Research 45:1387–1396. doi: 10.1139/cjfr-2015-0042.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. Mcdowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. T. Hogg, P. Gonzales, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat induced tree mortality reveals emerging climate change risk for forests. Forest Ecology and Management 259:660–684.

Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:129. http://dx.doi.org/10.1890/ ES15-00203.1

Allen, G. S. 1942. Douglas-fir seed from young trees. Journal of Forestry 40:722–723.

Allen, G. S., and J. N. Owens. 1972. The Life History of Douglas-fir. Environmental Canada Forestry Service, Ottawa, Canada.

Anderson, L., C. Carlson, and R. Wakimoto. 1987. Forest fire frequency and western spruce budworm outbreaks in western Montana. Forest Ecology and Management 22:251–260.

Arbellay, E., P. Fonti, and M. Stoffel. 2012. Duration and extension of anatomical changes in wood structure after cambial injury. Journal of experimental botany 63:3271–3277.

Axelson, J. N., A. Bast, R. Alfaro, D. J. Smith, and H. Gärtner. 2014. Variation in wood anatomical structure of Douglas-fir defoliated by the western spruce budworm: a case study in the coastal-transitional zone of British Columbia, Canada. Trees 28:1837–1846.

Axelson, J. N., D. J. Smith, L. D. Daniels, and R. I. Alfaro. 2015. Multicentury reconstruction of western spruce budworm outbreaks in central British Columbia, Canada. Forest Ecology and Management 335:235–248.

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

(BCMFR) British Columbia Ministry of Forests and Range. 2007. Timber Supply and the Mountain Pine Beetle Infestation in British Columbia: 2007 Update. URL: http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/Pine_Beetle_Update20070917.pdf [Accessed March 2014].

(BCMFR) British Columbia Ministry of Forests and Range. 1995. Defoliator Management Guidebook. URL: http://www.for.gov.bc.ca/tasb/legsregs/fpc/fpcguide/defoliat/defoltoc.htm [Accessed June 2014].

Battisti, A. 2008. Forests and climate change–lessons from insects. iForest 1:1–5.

Begum, S., S. Nakaba, Y. Yamagishi, Y. Oribe, and R. Funada. 2013. Regulation of cambial activity in relation to environmental conditions: Understanding the role of temperature in wood formation of trees. Physiologia Plantarum 147:46–54.

Berryman, A. A. 1996. What causes population cycles of forest Lepidoptera. Trends in Ecology & Evolution 11:28–32.

Bigio, E., H. Gärtner, and M. Conedera. 2010. Fire-related features of wood anatomy in a sweet chestnut (*Castanea sativa*) coppice in southern Switzerland. Trees - Structure and Function 24:643–655.

Blais, J. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Canadian Journal of Forest Research 13:539–547.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.

Boulanger, Y., and D. Arseneault. 2004. Spruce budworm outbreaks in eastern Quebec over the last 450 years. Canadian Journal of Forest Research 34:1035–1043.

Boulanger, Y., D. Arseneault, H. Morin, Y. Jardon, P. Bertrand, and C. Dagneau. 2012. Dendrochronological reconstruction of spruce budworm (*Choristoneura fumiferana*) outbreaks in southern Quebec for the last 400 years. Canadian Journal of Forest Research 42:1264–1276.

Bradley, A. F., W. C. Fischer, and N. V. Noste. 1992. Fire Ecology of the Forest Habitat Types of Eastern Idaho and Western Wyoming. USDA Forest Service Intermountain Research Station General Technical Report INT-290, Ogden, UT.

Brix, H. 1972. Nitrogen Fertilization and water effects on photosynthesis and earlywood–latewood production in Douglas-fir. Canadian Journal of Forest Research 2:467–478.

Brix, H., and A. Mitchell. 1980. Effects of thinning and nitrogen fertilization on xylem development in Douglas-fir. Canadian Journal of Forest Research 10:121–128.

Bryan, J. A., and R. M. Lanner. 1981. Epicormic branching in Rocky Mountain Douglas-fir. Canadian Journal of Forest Research 11:190–200.

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

Bunn, A., M. Korpela, F. Biondi, F. Campelo, P. Merian, F. Qeadan, and C. Zang. 2012. dplR: Dendrochronology program library in R. package version 1.5.6 URL http://www.cran.r-project.org/package=dplR [Accessed June 2014].

Burns, R., and B. Honkala. 1990. Silvics of North America Volume 2 : Softwoods. USDA Forest Service, Washington, DC.

Buxton K, and L. Maclauchlan. 2001-2014. Overview of Forest Health Conditions in Southern B.C. Ministry of Forests, Lands and Natural Resource Operations, Kamloops, B.C. URL http://www.for.gov.bc.ca/rsi/ForestHealth/Overview.htm. [Accessed June 2015].

Campbell, E., S. Saunders, D. Coates, D. Meidinger, A. MacKinnon, G. O'Neill, D. MacKillop, S. DeLong, and D. Morgan. 2009. Ecological Resilience and Complexity: a Theoretical Framework for Understanding and Managing British Columbia's Forest Ecosystems in a Changing Climate. Technical Reprot 055. B.C. Ministry of Forests and Range, Victoria, BC.

Campbell, R. 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. Ecology 60:1036–1050.

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

Campbell, R., D. Smith, and A. Arsenault. 2006. Multicentury history of western spruce budworm outbreaks in interior Douglas-fir forests near Kamloops, British Columbia. Canadian Journal of Forest Research 36:1758–1769.

Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: Resilience of what to what? Ecosystems 4:765–781.

Chapin, F. S., T. V Callaghan, Y. Bergeron, M. Fukuda, J. F. Johnstone, G. Juday, and S. Zimov. 2004. Global change and the boreal forest: thresholds, shifting states or gradual change? Ambio 33:361–365.

Chen, P.-Y., C. Welsh, and A. Hamann. 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. Global Change Biology 16:3374–3385.

Chen, Z., K. Clancy, and T. Kolb. 2003. Variation in budburst phenology of Douglas-fir Related to western spruce budworm (*Lepidoptera: Tortricidae*) fitness. Journal of Economic Entomology 96:377–387.

Clancy, K. M. 1992. The role of sugars in western spruce budworm nutritional ecology. Ecological Entomology 17:189–197.

Cooke, B. J., V. G. Nealis, and J. Régnière. 2007. Insect defoliators as periodic disturbances northern forest ecosystems. In: Plant Disturbance Ecology; The Processes and the Response. E. A. Johnson and K. Miyanishi (Eds.). Academic Press, London. pp. 487-525.

Cook, D. R. 1993. Partial residual plots. Technometrics 35:351–362.

Cook, E., P. Krusic, R. Holmes, and K. Peters. 2007. Program ARSTAN Version 41d. URL http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software [Accessed May 2013].

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

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

Copini, P., U. Sass-Klaassen, J. den Ouden, G. M. J. Mohren, and A. J. M. Loomans. 2014. Precision of dating insect outbreaks using wood anatomy: the case of Anoplophora in Japanese maple. Trees 28:103–113.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and M. Wottom. 2001. Climate change and forest disturbances. BioScience 51:723–734.

Dalla-Salda, G., A. Martinez-Meier, H. Cochard, and P. Rozenberg. 2009. Variation of wood density and hydraulic properties of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) clones related to a heat and drought wave in France. Forest Ecology and Management 257:182–189.

Dalla-Salda, G., A. Martinez-Meier, H. Cochard, and P. Rozenberg. 2011. Genetic variation of xylem hydraulic propperties shows that wood density is involved in adaptation to drought in Douglas-fir (*Pseudotsuga menziesii* (Mirb.)). Annal of Forest Scicne 68:747–757.

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

de Kort, I., V. Loeffen, and P. Baas. 1991. Ring width, density and wood anatomy of Douglas-fir with different crown vitality. IAWA Journal 12:453–465.

de Kort, I. 1993. Wood production and latewood percentage of Douglas-fir from different stands and vitality classes. Canadian Journal of Forest Research 23:1480–1486.

DeRose, R. J., and J. N. Long. 2014. Resistance and resilience: A conceptual framework for silviculture. Forest Science 60:1205–1212.

Deslauriers, A., H. Morin, and Y. Begin. 2003. Cellular phenology of annual ring formation of *Abies balsamea* in the Quebec boreal forest (Canada). Canadian Journal of Forest Research 33:190–200.

Devine, W. D., and C. A. Harrington. 2009. Relationships among foliar phenology, radial growth rate, and xylem density in a young Douglas-fir plantation. Wood and Fiber Science 41:300–312.

Diskin, M., M. E. Rocca, K. N. Nelson, C. F. Aoki, and W. Romme. 2011. Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. Canadian Journal of Forest Research 41:782–792.

Dodd, R. S., and P. Fox. 1990. Kinetics of tracheid differntiation in Douglas-fir. Annals of Botany 65:649–657.

Domec, J.-C., and B. L. Gartner. 2002. How do water transport and water storage differ in coniferous earlywood and latewood? Journal of Experimental Botany 53:2369–2379.

Drever, C. R., G. Peterson, C. Messier, Y. Bergeron, and M. Flannigan. 2006. Can forest management based on natural disturbances maintain ecological resilience? Canadian Journal of Forest Research 36:2285–2299.

El-Kassaby, Y. A., and H. J. Barclay. 1992. Cost of reproduction in Douglas-fir. Canadian Journal of Botany 70:1429–1432.

Ericsson, A., and J. Hellkvist. 1980. Consumption and pine growth: Hypotheses on effects on growth processes by needle-eating insects. Ecological Bulletins 32:537–545.

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

Fellin, D., and J. Dewey. 1982. Western Spruce Budworm. Forest Insect & Disease Leaflet 53. USDA, Forest Service.

Fettes, J.J. 1950. Investigations of sampling techniques for population studies of the spruce budworm on balsam fir in Ontario. Annual Technical Report 4, Sault Sainte Marie, ON.

Fettig, C. J., M. L. Reid, B. J. Bentz, S. Sevanto, D. L. Spittlehouse, and T. L. Wang. 2013. Changing Climates, changing forests: A western North American perspective. Journal of Forestry 111:214–228.

Fiddick, R.L., and G.A. van Sickle. 1979. Forest Insect and Disease Conditions, British Columbia and Yukon, 1979. Fisheries and Environment Canada, Canadian Forest Service, Pacific Forest Research Centre, Victoria, BC. Information Report BC-X-200.

Fielder, P., and J. N. Owens. 1989. A comparative study of shoot and root development of interior and coastal Douglas-fir seedlings. Canadian Journal of Forest Research 19:1210–1210.

Filion, L., and L. Cournoyer. 1995. Variation in wood structure of eastern larch defoliated by the larch sawfly in subarctic Quebec, Canada. Canadian Journal of Forest Research 25:1263–1268.

Fischer, J., D. B. Lindenmayer, and A. D. Manning. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment 4:80–86.

Flower, A., D. G. Gavin, E. K. Heyerdahl, R.A. Parsons, and G. M. Cohn. 2014. Drought-triggered western spruce budworm outbreaks in the interior Pacific Northwest: A multi-century dendrochronological record. Forest Ecology and Management 324:16–27.

Folke, C. 2006. Resilience: The emergence of a perspective for social–ecological systems analyses. Global Environmental Change 16:253–267.

Fox. J. 2003. Effect Displays in R for Generalised Linear Models. Journal of Statistical Software 8:1-27.

Fox, J., S. Weisberg, M. Friendly, J. Hong, R. Andersen, D. Firth, and S. Taylor. 2015. effects: Effect Displays for Linear, Generalized Linear, and Other Models. R library, v3.0-3. http://cran.r-project.org/web/packages/effects/index.html [Accessed May 2015].

Franceschi, V.R., P. Krokene, E. Christiansen, and T. Krekling. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytologist 167:353–376.

Freeman, T.N. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America I. Some new forms of *Choristoneura* allied to *C. fumiferana*. Canadian Entomologist 99:449–455.

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

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

Gartner, B.L., R. Aloni, R. Funada, A. N. Lichtfuss-Gautier, and F. A. Roig. 2002. Clues for dendrochronology from studies of wood structure and function. Dendrochronologia 20:53–61.

Gärtner, H., and F. Schweingruber. 2013. Microscopic Preparation Techniques for Plant Stem Analysis. Verlag Dr. Kessel, Remagen.

Gärtner, H., S. Lucchinetti, and F. H. Schweingruber. 2014. New perspectives for wood anatomical analysis in dendrosciences: The GSL1-microtome. Dendrochronologia 32:47–51.

Giraudoux, P. 2013. Pgirmess**:** data analysis in ecology. R package version 1.5.8. URL http://cran.r-project.org/web/packages/pgirmess/index.html [Accessed May 2014].

Green, R., and K. Klinka. 1994. A field guide to site identification and interpretation for the Vancouver Forest Region. Land Management Handbook No. 28. B.C. Ministry of Forests, Victoria, BC.

Griesbauer, H. P., and D. S. Green. 2010. Regional and ecological patterns in interior Douglas-fir climate–growth relationships in British Columbia, Canada. Canadian Journal of Forest Research 40:308–321.

Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109:323–334.

Grotta, A. T., B.L. Gartner, S.R. Radosevich, and M. Huso. 2005. Influence of red alder competition on cambial phenology and latewood formation in Douglas-fir. IAWA Journal 26:309–324.

Gunderson, L. H. 2000. Ecological resilience in theory and application. Annual Review of Ecology and Systematics 31:425–439.

Hadley, K., and T. Veblen. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. Canadian Journal of Forest Research 23:479–491.

Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. BioScience 41:382–392.

Harris, J., R.I. Alfaro, A. Dawson, and R. Brown. 1985. The western spruce budworm in British Columbia 1909–1983. Information Report BC-X-257. Canadian Forest Service, Pacific Forestry Centre, Victoria, BC.

Hedlin, A. F. 1964. A six-year plot study on Douglas-fir cone insect population fluctuations. Forest Science 10:124–128.

Helms, J.A. 1998. Dictionary of Forestry. Society of American Foresters and CABI Publishing, Cambridge, MA.URL http://www.dictionaryofforestry.org/ [Accessed June 2015].

Hessburg, P. F., R. G. Mitchell, and G. M. Filip. 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forested landscapes. USDA. Forest Service. Pacific Northwest Research Station, Portland, Oregon.

Holling, C. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Holling, C. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62:447–502.

Holling, C.S., and L.H. Gunderson. 2002. Resilience and adaptive cycles. In: Panarchy. L.H. Gunderson, and C.S. Holling (Eds.) Island Press, Washington, pp. 25–62.

Holmes, R. 1986. Users manual for program COFECHA. In: Tree- ring chronologies of western North America: California, eastern Oregon and northern Great Basin. R. L. Holmes, R. K. Adams, and H. C. Fritts (Eds.). Chronol. Ser. VI. University of Arizona, Tucson, AZ.

Holmes, R., and T. Swetnam. 1996. Program OUTBREAK Users manual, dendrochronology program library. Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ.

Hope, G. A., W. R. Mitchell, D. A. Lloyd, W. R. Erickson, W. L. Harper, and B. M. Wikeem. 1991. Chapter 10: Interior Douglas-fir zone. In: Ecosystems of British Columbia. D. Meidinger and J. Pojar (Eds.). B.C. Ministry of Forests,Victoria, BC, pp.153–166.

S.H. Hurlbert. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

Jardon, Y., H. Morin, and P. Dutilleul. 2003. Périodicité et synchronisme des épidémies de la tordeuse des bourgeons de l'épinette au Québec. Canadian Journal of Forest Research 33:1947–1961.

Johnson, G. R., B. L. Gartner, D. Maguire, and A. Kanaskie. 2003. Influence of Bravo fungicide applications on wood density and moisture content of Swiss needle cast affected Douglas-fir trees. Forest Ecology and Management 186:339–348.

Johnson, G. R., A. T. Grotta, B. L. Gartner, and G. Downes. 2005. Impact of the foliar pathogen Swiss needle cast on wood quality of Douglas-fir. Canadian Journal of Forest Research 35:331–339.

Johnston, M., T. Williamson, and A. Munson, A. E. Ogden, M. T. Moroni, R. Parsons, D. Price, and J. Stadt. 2010. Climate change and forest management in Canada: Impacts, adaptive capacity and adaptation options. A State of Knowledge report. Sustainable Forest Management Network, Edmonton, AB

Kaitaniemi, P., K. Ruohomaki, T. Tammaru, and E. Haukioja. 1999. Induced resistance of host tree foliage during and after a natural insect outbreak. Journal of Animal Ecology 68:382–389.

Kennedy, R.W. 1961. Variation and periodicity of summerwood in some second-growth Douglas-fir. Tappi 44: 161–166.

Kerkhoff, A. J., and B. J. Enquist. 2007. The implications of scaling approaches for understanding resilience and reorganization in ecosystems. BioScience 57:489–500.

Klenner, W., R. Walton, A. Arsenault, and L. Kremsater. 2008. Dry forests in the southern interior of British Columbia: Historic disturbances and implications for restoration and management. Forest Ecology and Management 256:1711–1722.

Kolb, B. T. E., M. R. Wagner, and W. W. Covington. 1994. Concepts of forest health. Journal of Forestry 92:10–15.

Koot, H.P. 1972. A conifer seedling weevil in British Columbia. FIDS Pest Leaflet No. 51. Environment Canada, Canadian Forestry Service, Pacific Forestry Centre, Victoria, BC.

Kozlowski, T.T., and T.A. Peterson. 1962. Seasonal growth of dominant, intermediate, and suppressed red pine trees. Botanical Gazette 124:146–154.

Kozlowski, T. 1969. Tree physiology and forest pests. Journal of Forestry 67:118–123.

Kramer, P. J. 1964. The role of water in wood formation. In: Formation of Wood in Forest Trees. M.H. Zimmermann (Ed.), Academic Press, NY, pp. 519–3532.

Krause, S., and K. Raffa. 1996. Differential growth and recovery rates following defoliation in related deciduous and evergreen trees. Trees 10:308–316.

Kulman, H. 1971. Effects of insect defoliation on growth and mortality of trees. Annual Review of Entomology 16:289–324.

Larocque, S., and D. Smith. 2003. Little Ice Age activity in the Mt. Waddington area, British Columbia coast mountains, Canada. Canadian Journal of Earth Sciences 40:1413–1436.

Larsen, W. A., and S. J. McCleary. 1972. THe use of partial residual plots in regression analysis. Technometrics 14:781–790.

Larson, P.R. 1962. Auxin gradients and the regulation of cambial activity. In: Tree Growth. T.T. Kozlowski (Ed.). The Ronald Press, New York, NY, pp. 97–117.

Larson, P.R. 1994. The Vascular Cambium. Development and Structure. Springer-Verlag, Berlin.

Lavender, D. P., and R. K. Hermann. 2014. Douglas-fir: The Genus *Pseudotsuga*. The Forestry Communictaions Group, Oregon State University, Corvallis, OR.

Lavigne, M. B., C. H. Little, and J. E. Major. 2001. Increasing the sink:source balance enhances photosynthetic rate of 1-year-old balsam fir foliage by increasing allocation of mineral nutrients. Tree physiology 21:417–426.

Lenth, R. V., and M. Hervé. 2015. Least-Squares Means, R library, v.2.18. http://cran.r-project.org/web/packages/lsmeans/index.html [Accessed May 2015].

Levin, S. A. 1992. The Problem of pattern and scale in ecology: The Robert H . MacArthur Award Lecture. Ecology 73:1943–1967.

Li, P., and W. Adams. 1994. Genetic variation in cambial phenology of coastal Douglas-fir. Canadian Journal of Forest Research 24:1864–1870.

Liang, C., L. Filion, and L. Cournoyer. 1997. Wood structure of biotically and climatically induced light rings in eastern larch (*Larix laricina*). Canadian Journal of Forest Research 27:1538–1547.

Liebhold, A., W. D. Koenig, and O. N. Bjørnstad. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology, Evolution, and Systematics 35:467–490.

Littell, J. S., D. L. Peterson, and M. Tjoelker. 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. Ecological Monographs 78:349–368.

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

Lloyd, D., K. Angrove, G. Hope and C. Thompson C. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. B.C. Ministry of Forests. Victoria, BC.

Lo, Y.-H., J. Blanco, B. Seely, C. Welham, and J. P. Kimmins. 2010. Relationships between climate and tree radial growth in interior British Columbia, Canada. Forest Ecology and Management 259:932–942.

Logan, J. A., J. Régnière, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment 1:130–137.

Lucas, J. and T. Lacourse. 2013. Holocene vegetation history and fire regimes of Pseudotsuga menziesii forests in the Gulf Islands National Park Reserve, southwestern British Columbia, Canada. Quaternary Research 79:366–376.

Lumley, L. M., and F. A. H. Sperling. 2011. Utility of microsatellites and mitochondrial DNA for species delimitation in the spruce budworm (*Choristoneura fumiferana*) species complex (*Lepidoptera: Tortricidae*). Molecular Phylogenetics and Evolution 58:232–243.

Lynch, A. 2012. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains In: Insect Outbreaks Revisited. P. Barbosa, D. K. Letourneau, and A. A. Agrawal (Eds.). Blackwell Publishing Ltd. Sussex, UK, pp.126–154.

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

Maclauchlan, L. E., J. E. Brooks, and J. C. Hodge. 2006. Analysis of historic western spruce budworm defoliation in south central British Columbia. Forest Ecology and Management 226:351–356.

Martínez-Cabrera, H. I., C. S. Jones, S. Espino, and H. Jochen Schenk. 2009. Wood anatomy and wood density in shrubs: Responses to varying aridity along transcontinental transects. American Journal of Botany 96:1388–1398.

Martinez-Meier, A., L. Sanchez, M. Pastorino, L. Gallo, and P. Rozenberg. 2008. What is hot in tree rings? The wood density of surviving Douglas-firs to the 2003 drought and heat wave. Forest Ecology and Management 256:837–843.

Martinez-Meier, A., L. Sanchez, G. Dalla-Salda, L. Gallo, M. Pastorino, and P. Rozenberg. 2009. Ring density record of phenotypic plasticity and adaptation to drought in Douglas-fir. Forest Ecology and Management 258:860–867.

Mason, R., B. Wickman, and H. Paul. 1997. Radial growth response of Douglas-fir and Grand Fir to larval densities of the Douglas-fir tussock moth and western spruce budworm. Forest Science 43:194–205.

McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends in Ecology and Evolution 26:523–532.

McLane, S. C., L. D. Daniels, and S. N. Aitken. 2011. Climate impacts on lodgepole pine (*Pinus contorta*) radial growth in a provenance experiment. Forest Ecology and Management 262:115–123.

Meidinger, D. and J. Pojar. 1991. Ecosystems of British Columbia. Special Report, Series 6. B.C. Ministry of Forest, Victoria, BC.

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

Moran, P. 1953. The statistical analysis of the Canadian lynx cycle. Australian Journal of Zoology 1:291–298.

Murdock, T. Q., S. W. Taylor, A. Flower, A. Mehlenbacher, A. Montenegro, F. W. Zwiers, R. Alfaro, and D. L. Spittlehouse. 2013. Pest outbreak distribution and forest management impacts in a changing climate in British Columbia. Environmental Science & Policy 26:75–89.

Myers, J. H. 1998. Synchrony in outbreaks of forest *Lepidoptera*: a possible example of the Moran effect. Ecology 79:1111–1117.

Nealis, V. G. 2012. The phenological window for western spruce budworm: seasonal decline in resource quality. Agricultural and Forest Entomology 14:340–347.

Nealis, V. G. 2015. Comparative ecology of conifer-feeding spruce budworms (Lepidoptera: Tortricidae). The Canadian Entomologist 25:1–25.

Nealis, V. G., and J. R. Nault. 2005. Seasonal changes in foliar terpenes indicate suitability of Douglas-fir buds for western spruce budworm. Journal of Chemical Ecology 31:683–696.

Nealis, V. G., and J. Régnière. 2013. An individual-based phenology model for western spruce budworm (Lepidoptera: Tortricidae). The Canadian Entomologist 146:306–320.

Nealis, V. G., M. K. Noseworthy, R. Turnquist, and V. R. Waring. 2009. Balancing risks of disturbance from mountain pine beetle and western spruce budworm. Canadian Journal of Forest Research 39:839–848.

O'Laughlin, J., and P. Cook. 2003. Inventory-based forest health indicators: Implications for national forest managment. Journal of Forestry:11–17.

Økland, B., A. M. Liebhold, O. N. Bjørnstad, N. Erbilgin, and P. Krokene. 2005. Are bark beetle outbreaks less synchronous than forest *Lepidoptera* outbreaks? Oecologia 146:365–372.

Oliver, C.D. 1980. Forest development in North America following major disturbances. Forest Ecology and Management 3:153–168.

Owens, J. N. 1968. Initiation and development of leaves in Douglas-fir. Canadian Journal of Botany 46:271–278.

Owens, J. N. 1973. The reproductive cycle of Douglas-fir. Pacific Forestry Research Centre, Victoria, B.C.

Owens, J. N. 1969. The relative importance of initiation and early development on cone production in Douglas-fir. Canadian Journal of Botany 47:1039–1049.

Owens, J., and M. Molder. 1971. Pollen development in Douglas-fir (*Pseudotsuga menziesii*). Canadian Journal of Botany 49:1263–1266.

Owens, J. N., and M. Molder. 1973. A study of DNA and mitotic activity in the vegetative apex of Douglas-fir during the annual growth cycle. Canadian Journal of Botany 51:1395–1409.

Owens, J., and S. Simpson. 1986. Pollen from conifers native to British Columbia. Canadian Journal of Forest Research 16:955–967.

Panshin, A. J. and C. de Zeeuw. 1980. Textbook of Wood Technology, 4th ed., McGraw and Hill, New York, NY.

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

Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1:6–18.

Pfister, R.D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest Habitat Types of Montana. USDA Forest Service General Technical Report INT-34. Intermountain Research Station, Ogden, Utah.

Piene, H., and C. Little. 1990. Spruce budworm defoliation and growth loss in young balsam fir: artifiical defoliation of potted trees. Canadian Journal of Forest Research 20:902–909.

Piene, H., and D. MacLean. 1999. Spruce budworm defoliation and growth loss in young balsam fir: patterns of shoot, needle and foliage weight production over a nine-year outbreak cycle. Forest Ecology and Management 123:115–133.

Pinheiro, J. C. and D. M. Bates. 2000. Mixed-Effects Models in S and S-PLUS. Springer-Verlag, New York, NY.

Pinheiro, J. C. and D. M. Bates., S. DebRoy, D. Karkar. 2015. nlme: Linear and Nonlinear Mixed Effects Models, R library, v3.1-12. http://cran.r-project.org/web/packages/nlme/index.html [Accessed June 2015].

Piñol, J., and A. Sala. 2000. Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northern USA. Functional Ecology 14:538–545.

Polák, T., B. N. Rock, P. Entheva Campbell, J. Soukupová, B. Solcová, K. Zvára, and J. Alberchtová. 2006. Shoot growth processes, assessed by bud development types, reflect Norway spruce vitality and sink prioritization. Forest Ecology and Management 225:337-348.

Pothier, D., and D. Mailly. 2006. Stand-level prediction of balsam fir mortality in relation to spruce budworm defoliation. Canadian Journal of Forest Research 36:1631–1640.

Poyatos, R., D. Aguadé, L. Galiano, M. Mencuccini, and J. Martínez-Vilalta. 2013. Drought-induced defoliation and long periods of near-zero gas exchange play a key role in accentuating metabolic decline of Scots pine. New Phytologist 200:388–401.

Pritzkow, C., I. Heinrich, H. Grudd, and G. Helle. 2014. Relationship between wood anatomy, tree-ring widths and wood density of Pinus sylvestris L. and climate at high latitudes in northern Sweden. Dendrochronologia 32:295–302.

Province of British Columbia. 2010. Field Manual for Describing Terrestrial Ecosystems, 2nd edition. Land management Handbook 25. B.C. Ministry of Forests and Ministry of Environment, Victoria, BC.

Puettmann, K. J., C. Messier, and D. K. Coates. 2013. Managing forests as complex adaptive systems. In: Managing forests as complex adaptive systems: Building resilience to the challenge of global change. C. Messier, K. J. Puettmann, D. K. Coates (Eds.) Routledge, New York, NY, pp. 3–16.

Quinn, G., and M. Keough. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, UR: http://www.R-project.org/ [Accessed June 2014].

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. BioScience 58:501–517.

Rais, A., J.-W. G. van K. De, and H. Pretzsch. 2014. Growth reaction patterns of tree height , diameter , and volume of Douglas-fir (*Pseudotsuga menziesii* [Mirb .] Franco) under acute drought stress in southern Germany. European Journal of Forest Research 133:1043–1056.

Rathgeber, C., V. Decoux, and J.-M. Leban. 2006. Linking intra-tree-ring wood density variations and tracheid anatomical characteristics in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Annals of Forest Science 63:699–706.

Razowski, J. 2008. Tortricidae (*Lepidoptera*) from South Africa. 6: *Choristoneura* Hübner and Procrica Diakonoff. Polish Journal of Entomology 77:245–254.

Reich, P., M. Walters, S. Krause, D. Vanderklein, K. Raffar, and T. Tabone. 1993. Growth, nutrition and gas exchange of *Pinus resinosa* following artificial defoliation. Trees 7:67–77.

Renninger, H., B. Gartner, and A. Grotta. 2006. No correlation between latewood formation and leader growth in Douglas-fir saplings. IAWA Journal 27:183–191.

Robertson, E. O., L. A. Jozsa, and D. L Spittlehouse. 1990. Estimating Douglas-fir wood production from soil and climatic data. Canadian Journal of Forest Research 20:357–364.

Romme, W. H., D. H. Knight, and J. B. Yavitt. 1986. Mountain pine beetle outbreaks in the rocky mountains: regulators of primary productivity? American Naturalist 127:484–494.

Rossi, S., A. Deslauriers, T. Anfodillo, H. Morin, A. Saracino, R. Motta, and M. Borghetti. 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. The New Phytologist 170:301–310.

Rossi, S., S. Simard, A. Deslauriers, and H. Morin. 2009. Wood formation in *Abies balsamea* seedlings subjected to artificial defoliation. Tree Physiology 29:551–558.

Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. Ecological Monographs 54:429–462.

Ruiz Diaz Britez, M., A.-S. Sergent, A. Martinez Meier, N. Bréda, and P. Rozenberg. 2014. Wood density proxies of adaptive traits linked with resistance to drought in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Trees 28:1289–1304.

Ryerson, D. E., T. W. Swetnam, and A. M. Lynch. 2003. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, U.S.A. Canadian Journal of Forest Research 33:1010–1028.

Saffell, B. J., F. C. Meinzer, D. R. Woodruff, D. C. Shaw, S. L. Voelker, B. Lachenbruch, and K. Falk. 2014. Seasonal carbohydrate dynamics and growth in Douglas-fir trees experiencing chronic, fungal-mediated reduction in functional leaf area. Tree Physiology 34:218–228.

Sainte-Marie, G. B., D. D. Kneeshaw, D. A. Maclean, and C. R. Hennigar. 2015. Estimating forest vulnerability to the next spruce budworm outbreak: will past silvicultural efforts pay dividends? Canadian Journal of Forest Research 45:314–324.

Sala, A., D. R. Woodruff, and F. C. Meinzer. 2012. Carbon dynamics in trees: Feast or famine? Tree Physiology 32:764–775.

Schneider, L., and H. Gärtner. 2013. The advantage of using a starch based non-Newtonian fluid to prepare micro sections. Dendrochronologia 31:175–178.

Schowalter, T. D. 1981. Insect herbivore relationship to the state of the host plant: biotic regulation of ecosystem nutrient cycling through ecological succession. Oikos 37:126–130.

Schowalter, T. D. 2011. Insect Ecology An Ecosystems Approach. 3rd Edition. Elsevier/Academic, San Diego, CA. doi:10.1016/B978-0-12-381351-0.00019-6

Schowalter, T., W. Hargrove, and D. A. Crossley, Jr. 1986. Herbivory in forested ecosystems. Annual Review of Entomology 31:177–196.

Shepherd, R. F. 1977. A classification of western Canadian defoliating forest insects by outbreak spread characteristics and habitat restriction. Insect Ecol. Agric. Exp. Sta. U. Minn. Tech. Bull. 310:80–88.

Shepherd, R. F., J. W. E. Harris, G. A. Van Sickle, L. H. Fiddick, and L. McMullen. 1977. Status of western spruce budworm on Douglas-fir in British Columbia. FIDS Pest Report September, Victoria, B.C

Shepherd, R. F., T. G. Gray, and T. F. Maher. 1992. Management of Black Army Cutworm. Pacific and Yukon Region, Information Report BC-X-335. Forestry Canada, Pacific Forestry Centre, Victoria, BC.

Shepherd, R. F. 1994. Management strategies for forest insect defoliators in British Columbia. Forest Ecology and Management 68:303–324.

Sibold, J. S., T. T. Veblen, K. Chipko, L. Lawson, E. Mathis, and J. Scott. 2007. Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. Ecological Applications 17:1638–1655.

Silen, R. R. 1978. Genetics of Douglas-fir. USDA Forest Service Research Paper. WO-35.

Simard, S. W. 2009. The foundational role of mycorrhizal networks in self-organization of interior Douglas-fir forests. Forest Ecology and Management 258:95–107.

Simpson, D. G. 2000. Water use of interior Douglas-fir. Canadian Journal of Forest Research 30:534–547.

Smith, D. M. 1962. The Practice of Silviculture. 7th Edition. John Wiley and Sons, Inc. New York, NY.

Sperry, J. S, U.G. Hacke, J, Pittermann. 2006. Size and function in conifer tracheids and angiosperm vessels. American Journal of Botany 93:1490–1500.

Spittlehouse, D. 2008. Climate change, impacts, and adaptation scenarios: climate change and forest and range management in British Columbia. Technical Report 045. British Columbia Ministry of Forests and Range, Victoria, BC.

Starheim, C. C. A., D. J. Smith, and T. D. Prowse. 2013. Dendrohydroclimate reconstructions of July – August runoff for two nival-regime rivers in west central British Columbia. Hydrological Processes 27:405-420. doi: 10.1002/hyp.9257

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

Stokes, M. and T. Smiley. 1968. An Introduction to Tree-Ring Dating. University of Chicago Press, Chicago, IL.

Swetnam, T., and A. Lynch. 1989. A tree-ring reconstruction of western spruce budworm history in the Southern Rocky Mountains. Forest Science 35:962–986.

Swetnam, T., and P.M. Brown. 1992. Oldest known conifers in the southwestern United States: temporal and spatial patterns of maximum age. Old Growth Forests in the Southwest and Rocky Mountain Regions. USDA Forest Service General Technical Report RM-213.

Swetnam, T., and A. Lynch. 1993. Mulicentury regional-scale patterns of western spruce budworm outbreaks. Ecological Monographs 63:399–424.

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

Sulak, A., and L. Huntsinger. 2012. Perceptions of forest health among stakeholders in an adaptive management project in the Sierra Nevada of California. Journal of Forestry 110:312–317.

Taylor S. W, A.L. Carroll, R.I. Alfaro, and L. Safranyik. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. In: The mountain pine beetle: a synthesis of biology, management, and impacts in lodgepole pine. L. Safranyik and W.R. Wilson (Eds.) Natural Resources Canada, Victoria B.C., pp 67–94.

Temperli, C., S. J. Hart, T. T. Veblen, D. Kulakowski, J. J. Hicks, and R. Andrus. 2014. Are density reduction treatments effective at managing for resistance or resilience to spruce beetle disturbance in the southern Rocky Mountains? Forest Ecology and Management 334:53–63.

Thomson, A., and G. Van Sickle. 1980. Estimation of tree growth losses caused by pest activity. Canadian Journal of Forest Research 10:176–182.

Thomson, A. J., and R. I. Alfaro. 1990. A method to calculate yield-correction factors for the overstorty component of budworm-attacked Douglas-fir. Forest Ecology and Management 31:255–267.

Thomson, A. J., and R. Benton. 2007. A 90-year sea warming trend explains outbreak patterns of western spruce budworm on Vancouver Island. The Forestry Chronicle 83:867–869.

Torrence, C., and G. Compo. 1998. A practical guide to wavelet analysis. Bulletin of the American Meteorological Society 79:61–78.

Uggla, C., E. Magel, T. Moritz, and B. Sundberg. 2001. Function and dynamics of auxin and carbohydrates during earlywood/latewood transition in Scots pine. Plant Physiology 125:2029–2039.

van Asch, M., and M. E. Visser. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. Annual Review of Entomology 52:37–55.

Van Sickle, G., R. Alfaro, and A. Thomson. 1983. Douglas-fir height growth affected by western spruce budworm. Canadian Journal of Forest Research 13:445-450.

Vargas-Hernandez, J., and W. Adams. 1994. Genetic relationships between wood density components and cambial growth rhythm in young coastal Douglas-fir. Canadian Journal of Forest Research 24:1871–1876.

Vincent, L., X. Wang, E. Milewska, H. Wan, F. Yang, and V. Swail. 2012. A second generation of homogenized Canadian monthly surface air temperature for climate trend analysis. Journal of Geophysical Research 117: D18110. doi:10.1029/2012JD017859.

Volney, J. A. 1994. Multi-century regional western spruce budworm outbreak patterns. Trends in Ecology & Evolution 9:43–45.

Volney, W. J. A., and K. G. Hirsch. 2005. Disturbing forest disturbances. The Forestry Chronicle 81:662–668.

Volney, W. J. A, and R. A. Fleming. 2007. Spruce budworm (*Choristoneura* spp.) biotype reactions to forest and climate characteristics. Global Change Biology 13: 1630–1643. doi:10.1111/j.1365-2486.2007.01402.x

Walker, I. and R. Sydneysmith. 2008. Chapter 8: British Columbia. In: From Impacts to Adaptation: Canada in a Changing Climate 2007. D.S. Lemmen, F.J. Warren, L. Lacroix, and E. Bush (Eds.), Government of Canada, Ottawa ON, pp. 329–386.

Wallner, W. 1987. Factors affecting insect population dynamics: Differences between outbreak and non-outbreak species. Annual Review of Entomology 32:317–340.

Wang, T., A. Hamann, D. Spittlehouse S. Aitken. 2006. Development of scale-free climate data for western Canada for use in resource management. International Journal of Climatology 26:383–397.

Wang, T., A. Hamann, D. L. Spittlehouse, and T. Q. Murdock. 2012. ClimateWNA-high-resolution spatial climate data for western North America. Journal of Applied Meteorology and Climatology 51:16–29.

Waring, R. H. 1987. Characteristics of trees predisposed to die. BioScience 37:569–574.

Watson, E., and B. H. Luckman. 2002. The dendroclimatic signal in Douglas-fir and ponderosa pine tree-ring chronologies from the southern Canadian Cordillera. Canadian Journal of Forest Research 32:1858–1874.

Watson, E., and B. H. Luckman. 2004. Tree-ring based reconstructions of precipitation for the southern Canadian cordillera. Climatic Change 65:209–241.

Westfall, J., and T. Ebata. 2000-2014. Summary of forest health conditions in British Columbia. Pest Management Report Number 15. British Columbia Ministry of Forests and Range, Victoria, BC.

White, P. 1979. Pattern, process and natural disturbance in vegetation. Botanical Reviews 45:229–299.

White, P.S., and Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. In: The Ecology of Natural Disturbance and Patch Dynamics. S.T.A. Pickett, P.S. White (Eds.) Academic Press, New York, pp. 3–13.

White, P. S., J. Harrod, W. H. Romme, and J. Betancourt. 1999. Disturbance and temporal dynamics. In: Ecological Stewardship: a Common Reference for Ecosystem Management. N.C. Johnson, A.J. Malk, W.T. Sexton, R. Szaro (Eds.) Oxford University, Oxford, pp. 281–305.

Wickman, B. E., R. R. Mason, and G. C. Trostle. 1981. Douglas-fir tussock moth. Forest Insect & Disease Leaflet 86. USDA, Forest Service.

Wickman, B. E., R. R Mason, and H. G. Paul. 1992. Thinning and nitrogen fertilization in a grand fir stand infested with western spruce budworm. Part II: tree growth response. Forest Science 38:252–264.

Wickham, H. and W. Chang. 2013. ggplot2: An implementation of the Grammar of Graphics. R package version 0.9.3.1. URL http://cran.r-project.org/web/packages/ggplot2/index.html [Accessed May 2014].

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

Wimmer, R. 1995. Intra-annual cellular characteristics and their implications for modelling softwood density. Wood Fiber Science 27:413–420.

Wodzicki, T. 2001. Natural factors affecting wood structure. Wood Science and Technology:5–26.

Wong, C., B. Dorner, and H. Sandman. 2003. Estimating Historical Variability of Natural Disturbances in British Columbia. Land Management Handbook. No. 53. British Columbia Ministry of Forests, Research Branch, British Columbia Ministry of Sustainable Resource Management, Resource Planning Branch, Victoria, BC.

Woods, A., D. Heppner, and H. Kope. 2010. Forest health and climate change: a British Columbia perspective. The Forestry Chronicle 86:412–422.

Yamaguchi, D. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research 21:414–416.

Zahner, R. 1968. Water deficit and growth in trees. In: Water Deficits and Plant Growth. T.T. Kozlowski (Ed.) Academic Press, New York, NY, pp. 191–254.

Zang, C. 2012. bootRes: bootstrapped response and correlation funcitons. R package version 1.2.3. URL http://www.cran.r-project.org/web/packages/bootRes/index.html [Accessed June 2014].

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

Zang, C., and F. Biondi. 2015a. treeclim: numerical calibration of cliamte-proxy relationships. R package version 1.0.13. URL https://cran.r-project.org/web/packages/treeclim/index.html [Accessed June 2015]

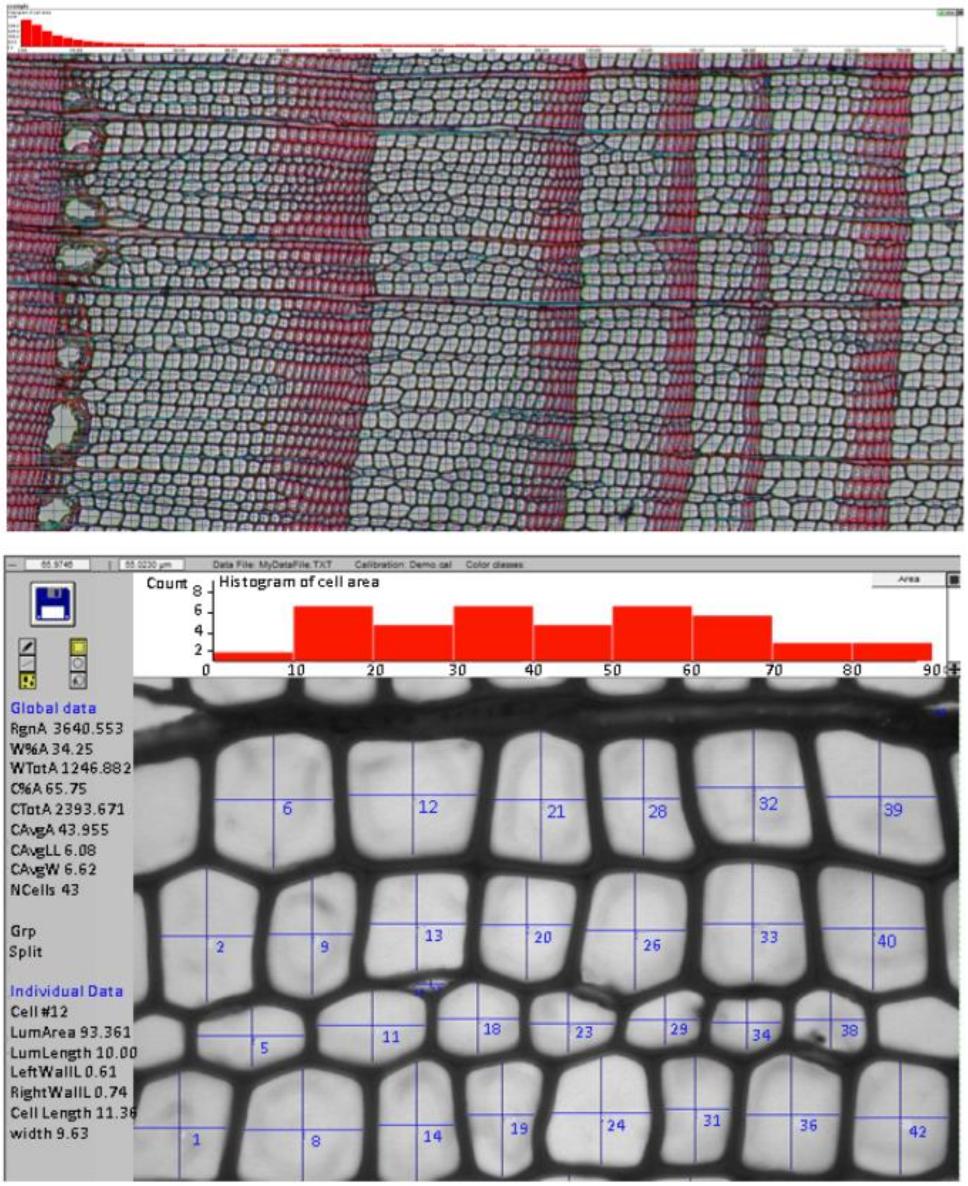
Zang, C., and F. Biondi. 2015b. Treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38:431–436.

Ziaco, E., F. Biondi, S. Rossi, and A. Deslauriers. 2014. Climatic influences on wood anatomy and tree-ring features of Great Basin conifers at a new mountain observatory. Applications in Plant Scienes 2:1–13.

Zobel, B., and J. van Buijtenen. 1989. Wood Variation: Its Causes and Control. Springer-Verlag, New York, NY.

Zuur, A., E.N. Ieno, N. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R, Springer, New York, NY.

Appendix I



```
Global data
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W%A 34.25
WTotA 1246.882
C%A 65.75
CTotA 2393.671
CAvgA 43.955
CAvgLL 6.08
CAvgW 6.62
NCells 43

Grp
Split

Individual Data
Cell #12
LumArea 93.361
LumLength 10.00
LeftWallL 0.61
RightWallL 0.74
Cell Length 11.36
width 9.63
```
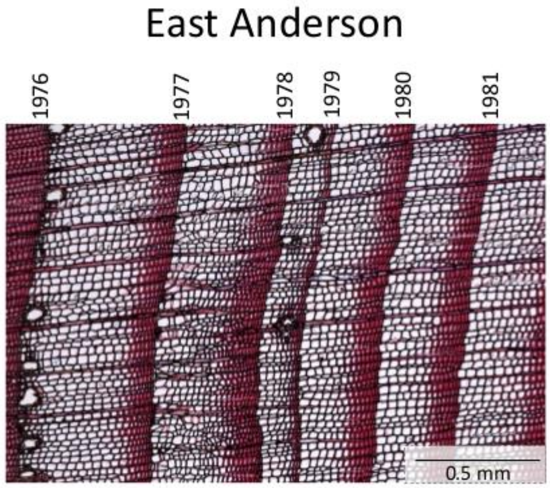
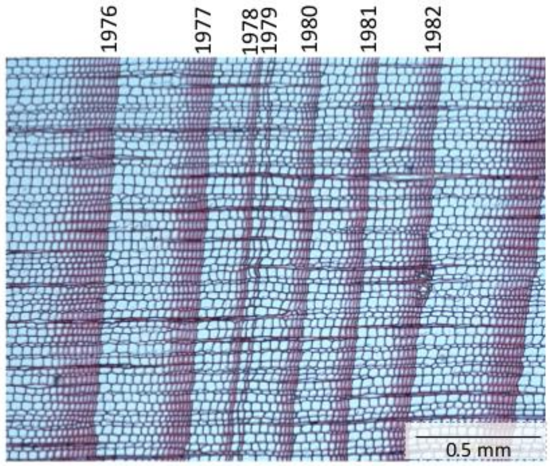

Figure A.1 Examples of measurements using the software package WinCell (Ver.2004a, Regents Instruments Inc. 2004). The top panel shows a global analysis across a micro section from Gilt Creek; the bottom panel shows individual cell measurements using the 'center' method, where the length and width of individual xylem cells are measured at the horizontal and vertical centers of each cell (bottom image from: http://regent.qc.ca/assets/wincell_measurements.html). The inset shows a schematic of how cell wall thickness is measured and averaged.



(a) Sample 2-7



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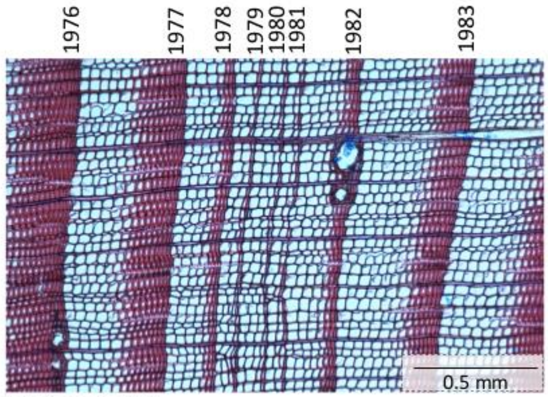
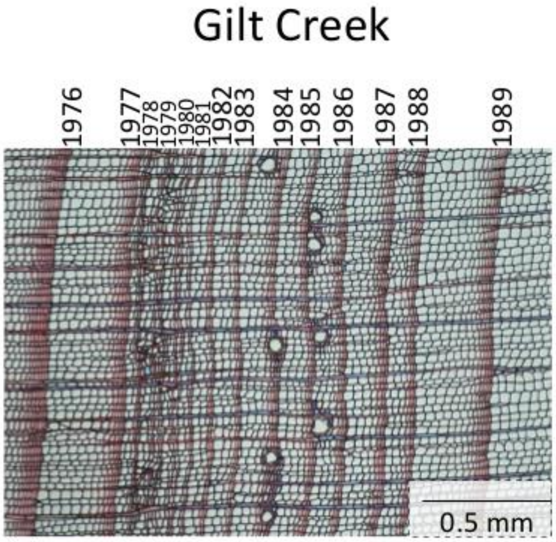


(c) Sample 5-5

Figure A.2 Example of micro section images for various samples from East Anderson, Fraser Canyon, British Columbia, Canada



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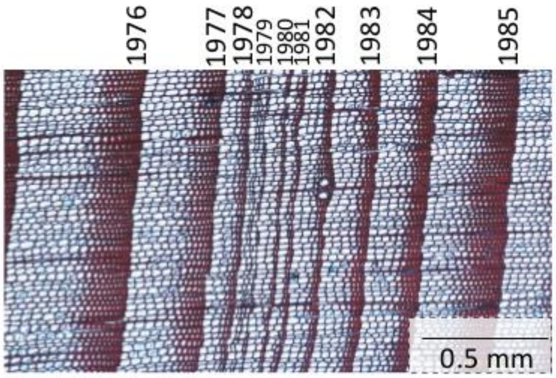
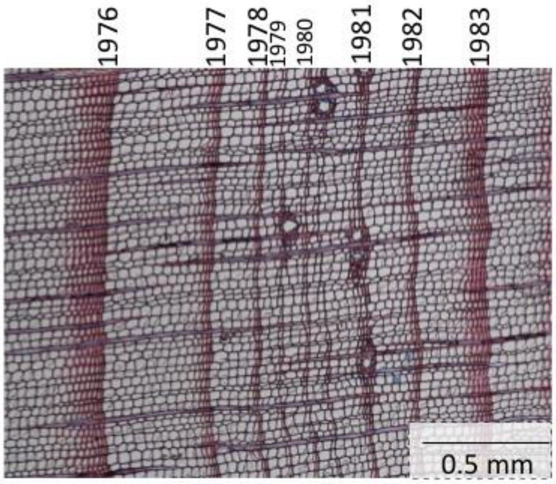


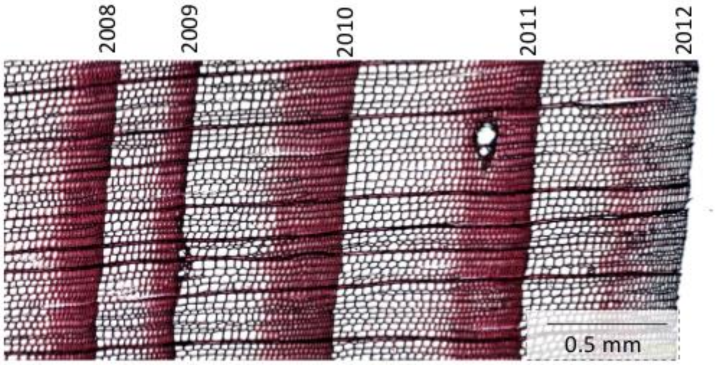
(b) Sample 4-7



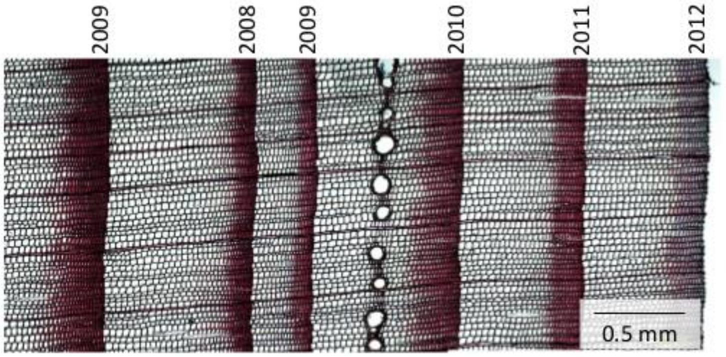
(c) Sample 4-17

Figure A.3 Example of micro section images for various samples from Gilt Creek, Fraser Canyon, British Columbia, Canada

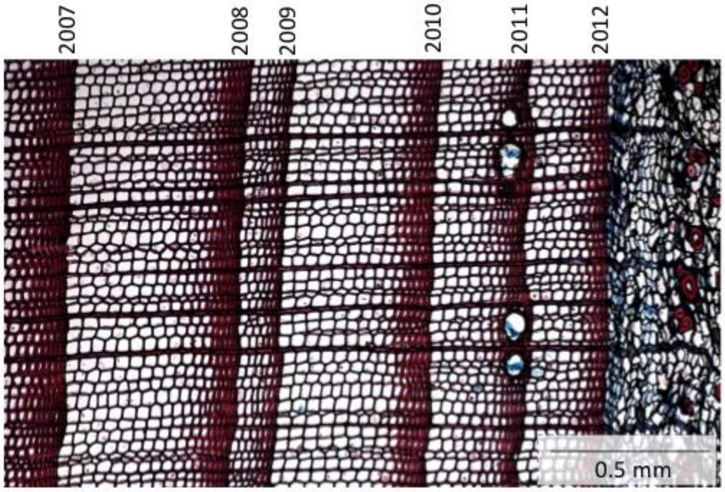
Site 3



(a) Sample 6



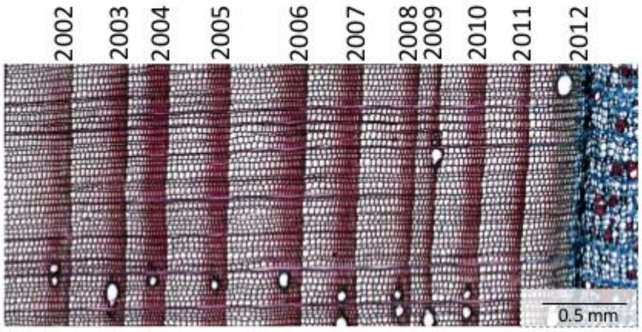
(b) Sample 10



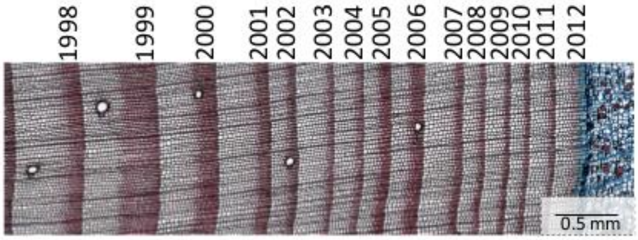
(c) Sample 11

Figure A.4 Example of micro section images for various samples from Site 3, Nicola Valley, southern interior of British Columbia, Canada.

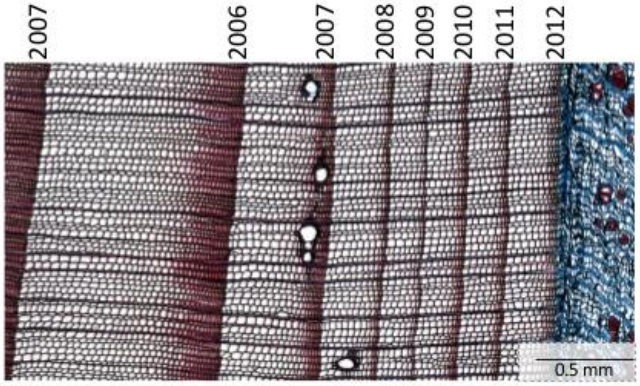
Site 4



(a) Sample 3



(b) Sample 8



(c) Sample 16

Figure A.5 Example of micro section images for various samples from Site 4, Nicola Valley, southern interior of British Columbia, Canada.

Table A.1 Tree sample depth, average ± standard deviation and minimum and maximum values per year for earlywood anatomical variables at East Anderson, Fraser Canyon, B.C., Canada. No defoliation occurred at the site from 1974-75 and 1984-86, defoliation averaged 50% (1976), 65% (1977), 60% (1978) and 20% (1980), post-outbreak period defined as 1981-83 (Fig. 4.2).

Year	Trees *N*	LA	Range (min – max)	CWT	Range (min – max)	RCD	Range (min – max)
1974	15	819.78 ± 142.99	577.50 – 1039.81	4.16 ± 0.45	3.44 – 4.95	38.98 ± 3.76	32.59 – 43.76
1975	20	876.24 ± 142.02	611.07 – 1115.46	4.16 ± 0.47	3.34 – 5.00	39.94 ± 3.62	31.50 – 45.22
1976	20	841.19 ± 140.08	528.31 – 1119.96	4.17 ± 0.45	3.33 – 5.00	38.85 ± 4.04	28.03 – 43.78
1977	20	847.67 ± 121.20	613.81 – 1073.02	4.04 ± 0.43	3.31 – 4.72	39.18 ± 3.39	36.07 – 46.53
1978	20	798.89 ± 176.78	397.07 – 1172.82	3.98 ± 0.42	3.14 – 4.80	36.95 ± 5.50	22.86 – 44.31
1979	20	786.33 ± 159.67	419.09 – 1032.52	3.91 ± 0.40	3.08 – 4.75	35.88 ± 5.06	25.88 – 45.02
1980	20	859.91 ± 149.62	632.82 – 1101.41	3.94 ± 0.36	3.23 – 4.69	38.41 ± 4.21	30.52 – 45.42
1981	20	879.64 ± 145.26	626.30 – 1124.71	3.96 ± 0.42	3.17 – 4.56	39.05 ± 3.67	31.23 – 44.77
1982	19	873.62 ± 154.66	653.98 – 1260.36	4.02 ± 0.39	3.26 – 4.71	38.69 ± 3.51	31.81 – 45.35
1983	17	841.96 ± 144.29	580.32 – 1131.76	3.95 ± 0.38	3.34 – 4.48	38.04 ± 3.14	32.14 – 43.69
1984	15	863.16 ± 142.46	645.39 – 1117.85	3.80 ± 0.37	3.19 – 4.33	37.98 ± 4.04	30.04 – 43.60
1985	13	884.88 ± 158.62	654.58 – 1204.83	3.91 ± 0.40	3.34 – 4.52	38.47 ± 3.95	30.29 – 43.08
1986	12	865.14 ± 114.23	710.12 – 1064.57	3.85 ± 0.33	3.25 – 4.26	38.24 ± 3.48	32.26 – 42.25

Abbreviations and units: LA=lumen area (μm^2), CWT=cell wall thickness (μm), RCD=radial cell diameter (μm).

Table A.2 Tree sample depth, average ± standard deviation and minimum and maximum values per year for latewood anatomical variables at East Anderson, Fraser Canyon, B.C., Canada. No defoliation occurred at the site from 1974-75 and 1984-86, defoliation averaged 50% (1976), 65% (1977), 60% (1978) and 20% (1980), post-outbreak period defined as 1981-83 (Fig. 4.2).

Year	Trees *N*	LA	Range (min – max)	CWT	Range (min – max)	RCD	Range (min – max)
1974	15	122.29 ± 27.85	74.27 – 160.19	6.69 ± 0.79	5.31 – 7.93	20.98 ± 2.36	15.60 – 24.70
1975	20	125.38 ± 26.53	81.30 – 176.26	6.33 ± 0.82	4.44 – 7.50	20.29 ± 2.38	14.14 – 23.21
1976	20	125.24 ± 18.13	89.54 – 149.30	6.11 ± 1.07	3.40 – 7.50	19.69 ± 2.87	13.24 – 23.94
1977	20	116.68 ± 24.49	75.02 – 157.86	5.73 ± 1.13	3.45 – 7.48	18.53 ± 3.14	11.87 – 23.33
1978	20	114.07 ± 21.39	76.19 – 151.71	4.98 ± 1.16	3.27 – 7.50	16.38 ± 2.73	12.24 – 21.29
1979	20	113.92 ± 26.97	73.34 – 158.49	4.83 ± 1.26	3.43 – 7.56	15.77 ± 3.05	10.73 – 21.33
1980	20	106.12 ± 20.95	67.53 – 147.41	5.82 ± 1.41	3.89 – 8.56	18.13 ± 3.51	12.58 – 24.24
1981	20	117.61 ± 24.30	71.48 – 163.64	6.13 ± 1.32	3.81 – 8.31	19.35 ± 3.50	12.65 – 25.12
1982	19	111.77 ± 27.42	75.17 – 175.48	6.44 ± 1.03	4.18 – 8.28	19.87 ± 2.53	14.66 – 23.85
1983	17	110.51 ± 23.31	79.86 – 155.95	6.58 ± 0.99	4.32 – 8.38	20.12 ± 2.29	14.87 – 22.19
1984	15	111.24 ± 21.02	83.18 – 164.25	6.37 ± 0.90	4.34 – 7.81	19.89 ± 2.48	13.67 – 23.38
1985	13	119.49 ± 29.39	94.48 – 209.12	6.35 ± 1.02	3.85 – 7.76	19.79 ± 2.96	12.76 – 23.23
1986	12	114.24 ± 21.92	81.92 – 146.18	6.46 ± 1.05	4.69 – 8.13	20.08 ± 2.67	15.20 – 23.23

Abbreviations and units: LA=lumen area (µm^2), CWT=cell wall thickness (µm), RCD=radial cell diameter (µm).

Table A.3 Tree sample depth, average ± standard deviation and minimum and maximum values per year for percent latewood at East Anderson, Fraser Canyon, B.C., Canada. No defoliation occurred at the site from 1974-75 and 1984-86, defoliation averaged 50% (1976), 65% (1977), 60% (1978) and 20% (1980), post-outbreak period defined as 1981-83 (Fig. 4.2).

Year	Trees *N*	Percent Latewood	Range (min – max)
1974	15	39.01 ± 5.58	30.30 – 48.66
1975	20	38.30 ± 5.92	28.08 – 49.27
1976	20	40.99 ± 9.09	27.23 – 66.60
1977	20	32.30 ± 9.85	18.25 – 50.33
1978	20	30.20 ± 11.84	16.58 – 69.27
1979	20	31.30 ± 11.60	16.00 – 56.45
1980	20	38.63 ± 11.45	13.42 – 57.00
1981	20	38.13 ± 7.24	27.00 – 54.28
1982	19	40.02 ± 9.33	25.78 – 58.00
1983	17	40.88 ± 9.70	23.84 – 61.25
1984	15	38.40 ± 8.73	28.00 – 54.33
1985	13	39.19 ± 8.01	20.92 – 50.25
1986	12	40.02 ± 7.79	29.54 – 56.2

Table A.4 Tree sample depth, average ± standard deviation and minimum and maximum values per year for earlywood anatomical variables at Gilt Creek, Fraser Canyon, B.C., Canada. No defoliation occurred at the site from 1974-75 and 1984-86, defoliation averaged 60% (1977) and ~58% (1978-79) (no data 1977 and 1980), post-outbreak period defined as 1981-83 (Fig. 4.2).

Year	Trees *N*	LA	Range (min – max)	CWT	Range (min – max)	RCD	Range (min – max)
1974	16	878.00 ± 173.16	627.04 – 1332.06	3.50 ± 0.52	2.59 – 4.61	38.55 ± 3.52	32.85 – 43.90
1975	16	868.18 ± 156.85	576.21 – 1080.11	3.60 ± 0.50	2.86 – 4.77	37.83 ± 3.37	31.54 – 42.82
1976	19	862.79 ± 126.00	531.28 – 1076.95	3.55 ± 0.40	2.94 – 4.61	37.64 ± 2.86	31.28 – 44.18
1977	19	807.06 ± 232.04	282.33 – 1135.66	3.40 ± 0.51	2.60 – 4.32	35.29 ± 6.19	19.35 – 45.17
1978	20	742.53 ± 223.10	203.74 – 1026.35	3.43 ± 0.50	2.57 – 4.28	33.17 ± 6.81	15.00 – 41.79
1979	19	764.72 ± 197.55	176.92 – 975.06	3.39 ± 0.46	2.55 – 4.18	34.16 ± 5.50	16.17 – 38.43
1980	20	803.18 ± 149.89	452.87 – 984.71	3.39 ± 0.45	2.63 – 4.24	35.38 ± 4.14	26.20 – 42.85
1981	20	818.66 ± 160.24	483.33 – 1026.23	3.37 ± 0.44	2.76 – 4.32	35.79 ± 4.07	27.37 – 42.56
1982	20	814.72 ± 146.43	541.83 – 1020.51	3.38 ± 0.44	2.63 – 4.44	35.59 ± 3.96	28.64 – 41.20
1983	19	809.84 ± 132.57	573.72 – 1051.95	3.24 ± 0.41	2.55 – 3.97	35.32 ± 3.53	29.32 – 40.71
1984	17	832.60 ± 186.01	544.53 – 1116.88	3.27 ± 0.38	2.65 – 4.22	35.16 ± 4.63	26.74 – 41.31
1985	17	825.84 ± 169.57	561.43 – 1063.58	3.38 ± 0.47	2.60 – 4.37	35.82 ± 4.34	27.77 – 41.66
1986	15	877.54 ± 200.01	449.12 – 1252.89	3.37 ± 0.46	2.65 – 4.12	36.63 ± 4.67	27.48 – 42.56

Abbreviations and units: LA=lumen area (μm^2), CWT=cell wall thickness (μm), RCD=radial cell diameter (μm).

Table A.5 Tree sample depth, average ± standard deviation and minimum and maximum values per year for latewood anatomical variables at Gilt Creek, Fraser Canyon, B.C., Canada. No defoliation occurred at the site from 1974-75 and 1984-86, defoliation averaged 60% (1977) and ~58% (1978-79) (no data 1977 and 1980), post-outbreak period defined as 1981-83 (Fig. 4.2).

Year	Trees *N*	LA	Range (min – max)	CWT	Range (min – max)	RCD	Range (min – max)
1974	16	138.03 ± 32.98	90.06 – 215.70	5.45 ± 0.93	3.78 – 7.31	19.37 ± 2.18	16.44 – 24.27
1975	16	136.42 ± 36.76	99.71 – 221.69	5.27 ± 0.68	4.25 – 6.46	18.54 ± 2.25	14.33 – 22.30
1976	19	144.62 ± 35.07	100.92 – 246.15	4.98 ± 0.69	3.79 – 6.59	18.51 ± 2.11	14.67 – 22.47
1977	19	116.99 ± 32.95	63.82 – 194.30	4.45 ± 0.78	2.91 – 5.89	15.95 ± 2.67	10.84 – 22.43
1978	20	112.07 ± 27.14	68.93 – 193.13	4.17 ± 0.98	2.56 – 6.72	14.89 ± 2.89	10.50 – 21.86
1979	19	113.94 ± 33.56	66.74 – 195.93	3.97 ± 0.87	2.85 – 5.49	14.46 ± 2.48	10.98 – 18.77
1980	20	122.99 ± 31.59	82.02 – 178.41	4.14 ± 0.93	2.82 – 6.72	15.36 ± 2.81	11.12 – 21.30
1981	20	119.72 ± 27.48	73.29 – 163.65	4.02 ± 0.72	3.04 – 5.75	15.13 ± 2.14	11.61 – 19.59
1982	20	114.15 ± 21.68	87.69 – 166.25	4.24 ± 0.99	2.94 – 6.09	15.47 ± 2.34	12.34 – 20.16
1983	19	123.06 ± 25.18	72.87 – 181.35	4.71 ± 1.27	2.96 – 6.72	16.79 ± 2.95	11.97 – 21.29
1984	17	133.20 ± 36.10	90.95 – 212.84	5.07 ± 1.37	2.76 – 7.43	17.89 ± 2.84	12.68 – 22.65
1985	17	121.88 ± 27.49	81.38 – 184.76	4.93 ± 1.24	3.17 – 6.56	17.35 ± 2.89	12.49 – 21.39
1986	15	124.57 ± 30.48	86.48 – 188.28	5.24 ± 1.52	3.13 – 8.63	17.92 ± 3.27	13.27 – 24.31

Abbreviations and units: LA=lumen area (μm^2), CWT=cell wall thickness (μm), RCD=radial cell diameter (μm).

Table A.6 Tree sample depth, average ± standard deviation, and minimum and maximum values per year for percent latewood at Gilt Creek, Fraser Canyon, B.C., Canada. No defoliation occurred at the site from 1974-75 and 1984-86, defoliation averaged 60% (1977) and ~58% (1978-79) (no data 1977 and 1980), post-outbreak period defined as 1981-83 (Fig. 4.2).

Year	Trees *N*	Percent Latewood	Range (min – max)
1974	16	31.66 ± 6.25	17.92 – 40.36
1975	16	30.50 ± 7.84	17.54 – 14.90
1976	19	33.74 ± 13.26	13.46 – 58.91
1977	19	28.89 ± 8.11	14.08 – 43.14
1978	20	27.83 ± 10.73	11.16 – 51.92
1979	19	29.05 ± 8.69	14.69 – 45.33
1980	20	28.13 ± 7.71	12.27 – 42.41
1981	20	28.37 ± 10.74	10.00 – 57.25
1982	20	31.71 ± 8.93	15.38 – 53.50
1983	19	29.99 ± 9.04	9.91 – 47.62
1984	17	33.74 ± 9.53	19.21 – 51.50
1985	17	32.18 ± 7.04	20.66 – 44.90
1986	15	30.53 ± 5.30	20.54 – 38.58

Table A.7 Tree sample depth, average ± standard deviation and minimum and maximum values per year for earlywood anatomical variables at Site 3, Nicola Valley, B.C., Canada. The frequency of defoliation for the 15-year analysis window was: 0% (1998); 1-25% (2004); >25-50% (1999, 2005); >50-75% (2010); and >75% (1997, 2000-03, 2006-09, 2011) (Fig. 5.3). Cumulative defoliation ranged from zero (no active budworm feeding) to a maximum of thirteen years continuous budworm feeding.

Year	Trees *N*	LA	Range (min – max)	CWT	Range (min – max)	RCD	Range (min – max)
1997	6	719.65 ± 52.64	657.54 – 791.52	4.15 ± 0.28	3.78 – 4.50	38.31 ± 1.74	36.32 – 40.85
1998	14	714.21 ± 110.73	538.83 – 886.65	4.04 ± 0.27	3.62 – 4.58	35.88 ± 3.12	29.15 – 39.76
1999	16	621.04 ± 119.26	466.01 – 914.76	4.01 ± 0.24	3.49 – 4.45	32.62 ± 3.57	27.06 – 39.33
2000	19	741.38 ± 124.63	492.45 – 932.31	4.09 ± 0.36	3.31 – 4.75	37.43 ± 3.69	29.55 – 42.25
2001	19	670.25 ± 110.39	481.31 – 878.26	4.07 ± 0.29	3.63 – 4.61	34.52 ± 3.76	26.24 – 40.64
2002	19	738.47 ± 120.12	562.23 – 959.22	4.00 ± 0.30	3.38 – 4.53	37.00 ± 3.32	30.52 – 45.05
2003	20	690.68 ± 87.37	553.03 – 843.51	3.95 ± 0.30	3.17 – 4.39	34.14 ± 3.35	28.39 – 39.47
2004	19	745.96 ± 149.53	536.93 – 1118.41	4.03 ± 0.28	3.55 – 4.53	37.01 ± 3.38	29.95 – 42.90
2005	19	651.68 ± 115.34	505.70 – 954.73	4.03 ± 0.34	3.22 – 4.76	34.15 ± 3.11	28.54 – 41.60
2006	20	781.97 ± 88.40	587.03 – 922.70	4.14 ± 0.31	3.41 – 4.56	38.48 ± 2.57	33.21 – 42.02
2007	18	743.36 ± 120.74	590.17 – 941.40	4.20 ± 0.31	3.65 – 4.83	36.76 ± 3.16	30.18 – 41.42
2008	18	781.31 ± 126.06	485.91 – 1033.96	4.10 ± 0.39	3.48 – 5.04	37.81 ± 4.14	26.55 – 44.93
2009	20	604.86 ± 139.37	367.20 – 868.25	3.88 ± 0.35	3.17 – 4.44	31.33 ± 4.65	22.82 – 40.41
2010	19	826.63 ± 149.04	639.18 – 1157.52	4.01 ± 0.34	3.43 – 4.87	39.22 ± 2.73	34.46 – 46.11
2011	19	779.61 ± 103.36	603.43 – 1037.77	4.06 ± 0.39	3.49 – 5.22	37.60 ± 3.27	31.05 – 45.51

Abbreviations and units: LA=lumen area (μm^2), CWT=cell wall thickness (μm), RCD=radial cell diameter (μm).

Table A.8 Tree sample depth, average ± standard deviation and minimum and maximum values per year for latewood anatomical variables at Site 3, Nicola Valley, B.C., Canada. The frequency of defoliation for the 15-year analysis window was: 0% (1998); 1-25% (2004); >25-50% (1999, 2005); >50-75% (2010); and >75% (1997, 2000-03, 2006-09, 2011) (Fig. 5.3). Cumulative defoliation ranged from zero (no active budworm feeding) to a maximum of thirteen years continuous budworm feeding.

Year	Trees *N*	LA	Range (min – max)	CWT	Range (min – max)	RCD	Range (min – max)
1997	6	102.82 ± 15.24	76.12 – 120.43	7.13 ± 0.79	5.94 – 8.19	21.36 ± 0.97	19.61 – 22.54
1998	14	101.01 ± 19.25	79.00 – 150.47	6.88 ± 0.65	5.83 – 7.78	20.69 ± 1.23	18.55 – 22.52
1999	16	105.16 ± 32.02	65.98 – 173.71	6.81 ± 0.67	5.65 – 8.15	20.61 ± 1.29	18.71 – 23.16
2000	19	102.81 ± 21.59	60.81 – 142.57	6.47 ± 0.55	5.49 – 7.35	19.59 ± 1.56	16.70 – 24.12
2001	19	111.59 ± 26.05	74.01 – 181.44	6.00 ± 0.53	4.90 – 6.87	18.94 ± 1.19	16.95 – 21.26
2002	19	102.29 ± 20.97	65.21 – 150.53	6.11 ± 0.56	5.15 – 7.26	18.71 ± 1.29	16.54 – 21.41
2003	20	102.17 ± 20.41	64.16 – 147.37	5.97 ± 0.76	4.87 – 7.42	18.18 ± 1.79	14.89 – 22.31
2004	19	98.11 ± 28.17	58.13 – 167.52	6.44 ± 0.64	4.63 – 7.45	19.24 ± 1.51	16.52 – 22.79
2005	19	106.03 ± 31.61	52.36 – 176.55	6.52 ± 0.63	5.61 – 7.70	20.00 ± 1.52	18.06 – 22.41
2006	20	109.27 ± 18.81	61.32 – 135.83	5.89 ± 0.62	4.76 – 7.10	18.41 ± 1.57	15.84 – 22.61
2007	18	102.53 ± 17.14	71.65 – 131.05	6.24 ± 0.60	5.13 – 7.36	19.00 ± 1.38	17.06 – 22.50
2008	18	119.41 ± 27.16	66.24 – 188.88	5.66 ± 0.51	4.75 – 6.52	18.09 ± 1.73	16.37 – 21.87
2009	20	111.11 ± 16.00	88.91 – 148.75	5.10 ± 0.52	4.01 – 6.08	16.45 ± 1.36	13.54 – 19.33
2010	19	106.25 ± 19.29	71.07 – 142.61	5.96 ± 0.74	3.98 – 7.11	18.46 ± 1.97	13.55 – 22.40
2011	19	111.91 ± 18.90	81.81 – 152.02	5.76 ± 0.82	4.29 – 7.40	17.98 ± 1.94	15.16 – 22.04

Abbreviations and units: LA=lumen area (µm^2), CWT=cell wall thickness (µm), RCD=radial cell diameter (µm).

Table A.9 Tree sample depth, average ± standard deviation and minimum and maximum values per year for percent latewood at Site 3, Nicola Valley, B.C., Canada. The frequency of defoliation for the 15-year analysis window was: 0% (1998); 1-25% (2004); >25-50% (1999, 2005); >50-75% (2010); and >75% (1997, 2000-03, 2006-09, 2011) (Fig. 5.3). Cumulative defoliation ranged from zero (no active budworm feeding) to a maximum of thirteen years continuous budworm feeding.

Year	Trees *N*	Percent Latewood	Range (min – max)
1997	6	41.34 ± 6.49	34.18 – 51.50
1998	14	40.91 ± 8.83	30.45 – 54.45
1999	16	51.17 ± 12.43	34.87 – 76.25
2000	19	39.39 ± 9.31	25.50 – 67.22
2001	19	42.33 ± 9.86	31.85 – 64.75
2002	19	31.48 ± 7.42	21.40 – 51.81
2003	20	39.85 ± 10.65	23.00 – 61.50
2004	19	41.47 ± 6.94	27.63 – 55.50
2005	19	43.62 ± 11.14	29.18 – 65.50
2006	20	30.52 ± 7.29	19.63 – 43.20
2007	18	41.03 ± 7.08	32.20 – 55.22
2008	18	29.05 ± 7.03	17.30 – 42.75
2009	20	41.94 ± 15.94	18.40 – 69.42
2010	19	31.73 ± 6.90	24.90 – 50.00
2011	19	32.54 ± 6.11	23.50 – 45.80

Table A.10 Site 4 tree sample depth, average ± standard deviation and minimum and maximum values per year for earlywood anatomical variables. The frequency of defoliation for the 15-year analysis window was: 0% (1997-98, 2002); 1-25% (1999, 2001, 2003); >25-50% (2000, 2004, 2008); >50-75% (2009, 2011); and >75% (2005-07, 2010) (Fig. 5.3). Cumulative defoliation at Site 4 ranged from 0 to a maximum of nine years of continuous budworm feeding.

Year	Trees *N*	LA	Range (min – max)	CWT	Range (min – max)	RCD	Range (min – max)
1997	15	731.35 ± 120.83	480.25 – 921.66	4.20 ± 0.42	3.32 – 4.74	36.95 ± 3.78	29.44 – 42.67
1998	16	725.97 ± 134.52	544.90 – 1041.42	4.29 ± 0.45	3.50 – 5.21	37.50 ± 4.17	30.38 – 47.39
1999	18	730.57 ± 144.89	428.17 – 983.40	4.23 ± 0.42	3.45 – 4.98	36.62 ± 4.44	26.76 – 43.74
2000	18	734.01 ± 116.73	554.23 – 998.06	4.16 ± 0.47	3.31 – 4.79	36.31 ± 3.88	28.02 – 43.92
2001	18	689.94 ± 103.07	450.64 – 880.24	4.16 ± 0.41	3.20 – 4.87	35.28 ± 3.22	27.13 – 40.44
2002	19	694.31 ± 112.85	421.26 – 866.18	4.21 ± 0.48	3.27 – 5.00	36.28 ± 3.89	26.78 – 43.32
2003	20	688.71 ± 108.87	439.66 – 863.83	4.12 ± 0.40	3.22 – 4.73	34.90 ± 3.57	27.49 – 40.39
2004	19	692.33 ± 148.92	364.81 – 964.19	4.10 ± 0.41	3.31 – 4.69	35.74 ± 4.19	24.87 – 43.26
2005	18	727.48 ± 125.63	446.32 – 1007.85	4.15 ± 0.48	3.23 – 5.12	36.38 ± 4.01	26.48 – 44.17
2006	19	764.46 ± 115.76	514.47 – 1056.25	4.19 ± 0.37	3.57 – 4.75	38.03 ± 3.81	28.70 – 46.88
2007	20	758.17 ± 93.13	522.08 – 915.85	4.19 ± 0.45	3.34 – 4.94	37.28 ± 3.13	29.68 – 42.68
2008	20	759.15 ± 125.99	500.92 – 1082.67	4.08 ± 0.48	3.14 – 4.88	36.28 ± 3.73	28.11 – 44.66
2009	20	699.86 ± 117.22	491.59 – 907.95	4.06 ± 0.54	3.16 – 5.10	34.51 ± 3.83	27.18 – 39.47
2010	19	774.05 ± 110.54	561.31 – 988.48	4.19 ± 0.53	3.32 – 5.42	37.11 ± 3.06	30.48 - 43.62
2011	20	707.68 ± 113.61	510.64 – 976.80	4.18 ± 0.55	3.30 – 5.31	35.71 ± 2.92	29.10 – 40.28

Abbreviations and units: LA=lumen area (μm^2), CWT=cell wall thickness (μm), RCD=radial cell diameter (μm).

Table A.11 Tree sample depth, average ± standard deviation and minimum and maximum values per year for latewood anatomical variables at Site 4, Nicola Valley, B.C., Canada. The frequency of defoliation for the 15-year analysis window was: 0% (1997-98, 2002); 1-25% (1999, 2001, 2003); >25-50% (2000, 2004, 2008); >50-75% (2009, 2011); and >75% (2005-07, 2010) (Fig. 5.3). Cumulative defoliation at Site 4 ranged from 0 to a maximum of nine years of continuous budworm feeding.

Year	Trees *N*	LA	Range (min – max)	CWT	Range (min – max)	RCD	Range (min – max)
1997	15	138.25 ± 30.87	92.62 – 214.37	5.98 ± 1.00	3.68 – 7.16	20.25 ± 2.65	13.60 – 24.45
1998	16	142.64 ± 29.33	110.63 – 201.71	6.22 ± 1.07	4.00 – 8.12	20.71 ± 2.33	15.77 – 24.61
1999	18	152.08 ± 21.73	122.39 – 204.82	6.06 ± 0.89	4.09 – 7.24	20.81 ± 2.08	17.15 – 24.53
2000	18	150.48 ± 28.63	114.49 – 223.38	5.82 ± 0.91	3.67 – 7.21	20.16 ± 2.26	15.27 – 23.84
2001	18	152.38 ± 34.77	113.94 – 256.44	5.29 ± 0.74	3.51 – 6.32	19.11 ± 1.87	14.42 – 21.38
2002	19	145.19 ± 33.85	91.33 – 201.55	5.34 ± 0.76	3.45 – 6.39	18.79 ± 2.48	13.41 – 22.23
2003	20	141.22 ± 26.21	98.62 – 186.01	5.30 ± 0.88	3.35 – 6.81	18.37 ± 1.99	13.65 – 21.70
2004	19	139.21 ± 38.73	78.26 – 217.77	5.78 ± 0.95	3.62 – 7.06	19.50 ± 2.65	12.93 – 25.07
2005	18	143.05 ± 24.30	106.81 – 198.91	6.26 ± 0.85	4.20 – 7.65	20.80 ± 2.25	15.54 – 25.45
2006	19	135.69 ± 20.68	97.64 – 185.41	5.83 ± 0.68	4.39 – 6.75	19.38 ± 1.88	15.71 – 26.67
2007	20	142.74 ± 27.29	106.46 – 209.56	5.61 ± 0.92	3.55 – 6.65	18.93 ± 2.40	14.05 – 23.89
2008	20	147.28 ± 27.13	108.24 – 208.31	5.20 ± 1.05	3.31 – 7.02	18.13 ± 2.67	13.15 – 24.35
2009	20	146.59 ± 20.62	109.23 – 180.22	4.81 ± 0.79	3.40 – 6.63	17.08 ± 2.08	13.31 – 21.51
2010	19	144.53 ± 21.69	108.27 – 214.44	6.00 ± 0.89	4.07 – 7.57	19.79 ± 2.42	15.52 – 24.34
2011	20	144.82 ± 40.00	89.14 – 245.28	6.09 ± 1.16	3.72 – 7.85	20.28 ± 2.97	13.25 – 25.19

Abbreviations and units: LA=lumen area (μm^2), CWT=cell wall thickness (μm), RCD=radial cell diameter (μm).

Table A.12 Tree sample depth, average ± standard deviation and minimum and maximum values per year for percent latewood at Site 4, Nicola Valley, B.C., Canada. The frequency of defoliation for the 15-year analysis window was: 0% (1997-98, 2002); 1-25% (1999, 2001, 2003); >25-50% (2000, 2004, 2008); >50-75% (2009, 2011); and >75% (2005-07, 2010) (Fig. 5.3). Cumulative defoliation at Site 4 ranged from 0 to a maximum of nine years of continuous budworm feeding.

Year	Trees *N*	Percent Latewood	Range (min – max)
1997	15	34.02 ± 10.67	21.20 – 59.50
1998	16	36.74 ± 8.47	20.77 – 52.60
1999	18	40.53 ± 12.40	17.80 – 68.40
2000	18	38.92 ± 12.08	19.70 – 66.75
2001	18	38.26 ± 12.63	21.72 – 67.45
2002	19	33.69 ± 11.32	17.00 – 55.77
2003	20	37.14 ± 13.05	18.62 – 67.60
2004	19	44.89 ± 11.30	23.71 – 73.22
2005	18	43.07 ± 6.49	29.20 – 50.40
2006	19	35.81 ± 11.20	16.58 – 59.00
2007	20	38.04 ± 11.35	19.41 – 67.36
2008	20	30.14 ± 12.44	15.91 – 64.00
2009	20	34.33 ± 13.95	15.46 – 62.66
2010	19	39.76 ± 11.37	21.84 – 63.80
2011	20	38.49 ± 10.44	24.06 – 66.25